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Succession and goose herbivory in monsoonal wetlands of the Keoladeo National Park, Bharatpur, India

by

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GENERAL ABSTRACT

Seasonal changes in vegetation in monsoonal wetlands in the Keoladeo National Park, Bharatpur, India, are related to changes in mean water depths which are lowest just before the onset of the monsoon (June 1984; <1 cm), highest immediately after the monsoon (October 1985; 89 cm). Water levels decline slowly over the winter (March 1985; 14 cm) and spring. The mean cover of the dominant species, *Paspalum distichum*, is lowest before the monsoon (June 1984; 19%), increases after the monsoon (October 1985; 35%), and reaches its peak in March (1985; 49%). Long term drought reduced the cover of *Paspalum distichum* to 2% (March 1987).

Grazing by Greylag (*Anser anser rubrirostris*) and Barheaded (*Anser indicus*) creates openings in the emergent vegetation. The mean distance to open areas, ie. areas free of vegetation, along grazed transects, before goose grazing was 193 m and after grazing, 43 m. For ungrazed transects, no change in mean distance to open water patches was observed during the same interval (344 m and 339 m, respectively). Seeds dispersed by the feeding and defecation of geese can potentially influence re-establishment of plants in openings.

Areas grazed by geese have a seed bank that contains 19-50 species per m^2 and a total of 3,425 - 16,195 seedlings

per m^2 as determined by the results of the moist soil and flooded treatments combined. During summer drawdown, annuals and seedlings of woody plants become established in open areas grazed by geese, but no seedlings of any species are found in ungrazed areas. The seed bank contains many species that were not found as adult plants in either grazed or ungrazed sites. Field observations, however, indicate that clonal growth of surviving individuals is primarily responsible for the re-establishment of vegetation in areas opened up by goose grazing, and that recruitment from the seed bank is only of secondary importance.

The food habits of overwintering Greylag (Anser anser rubrirostris) and Barheaded (Anser indicus) Geese are discussed for the Keoladeo National Park, Bharatpur, India. Greylag Geese eat mostly seeds of Nymphaea nouchali and Oryza rufipogon in November and December but shift to native grasses such as Paspalum distichum in January. They eat mostly P. distichum until they leave in March. Barheaded Geese eat mostly young wheat (Triticum aestivum) in January, native grasses, such as Paspalum distichum in February and change to field peas (Pisum sativum) and grams (Cicer arietinum) in March and April. Overall, Paspalum distichum is the most important species in the diet of these geese, comprising 67.8% of the Greylag and 45.8% of the Barheaded Goose diet. Decisions regarding the selection of species for clipping in garden and field studies were based on the food habits study.

In an experimental clipping study conducted in Bharatpur, India, four plant species were either clipped weekly, every two weeks, or left unclipped while growing at one of 3 water levels (0 cm, 3 cm, or 13 cm below the surface of the water). When clipped underwater, individuals of Ipomoea aquatica Forsk., Paspalidium punctatum A. Camus, and Paspalum distichum Linn., usually died but not those of Nymphoides cristatum Kuntze. In a companion field study in a monsoonal wetland in the nearby Keoladeo National Park, plants of Ipomoea aquatica and Paspalum distichum also usually died when clipped underwater.

In the experimental study, the total biomass of clipped plants including above- and below-ground biomass, for a given species depended on water depth and clipping frequency. Most species had less total biomass when clipped than unclipped. For example, plants of Paspalum distichum that were clipped every two weeks had less total biomass (5.4 g) than unclipped plants (9.5 g) in 0 cm of water. An exception, the total biomass of unclipped plants of Nymphoides cristatum (1.8 g), did not differ significantly from plants clipped every week and every two weeks in -3 cm water (1.1 and 1.4 g, respectively). In general, clipping reduced mean root mass and increased mean shoot mass.

GENERAL INTRODUCTION

As a determinant of the structure of wetlands of the prairie pothole region of North America, herbivory has been cited as second in importance only to water level changes (Weller 1978). Herbivory is responsible for the elimination of emergent vegetation and thus the onset of an open lake phase which persists until the next drought (van der Valk 1985). Herbivory may function similarly in sub-tropical and tropical wetlands but herbivory studies in monsoonal wetlands have been limited to observations made during studies on other topics (Gaudet 1977, McLachlan 1971).

The effect of waterfowl herbivory on primary production has been studied in temperate tidal and prairie pothole wetlands (Anderson and Low 1976, Jeffries et al. 1979, Smith and Odum 1981), but no similar studies have been conducted in monsoonal wetlands. This study examines the role of goose herbivory in a sub-tropical (Meher-Homji 1978) monsoonal wetland in India. More than six thousand Greylag, (*Anser anser*), and Barheaded Geese, (*Anser indicus*), use this wetland in the Keoladeo National Park, Bharatpur, Rajasthan, India as an overwintering area from October-April. The impact of these geese on the structure and functioning of the wetland will be explored in this study.

The questions asked here are:

1. what are the sizes, numbers, and characteristics of openings created by geese in the wetland?

2. how do geese create openings in the aquatic vegetation of monsoonal wetlands?

3. how are these openings revegetated?

To answer these questions, three studies were done:

1. the vegetation was surveyed, as were the locations and sizes of openings associated with goose grazing and the seed banks of the wetland,

2. the food habits of the geese were studied,

3. goose grazing was simulated by mechanical clipping to examine the effect of grazing on the survival and growth of aquatic plants.

The food habits study presented in Section 1 published as, "Food habits of Greylag and Barheaded Geese in the Keoladeo National Park, Bharatpur, India" (Middleton and van der Valk 1987). Plant cutting underwater is used to kill aquatic weeds (Nichols 1971) and herbivory also may lead to the death or slow growth of plants. The experimental and field response of plants clipped underwater is tested in Section 2, "Effect of water depth and clipping frequency on the growth and survival of four wetland plant species". Section 3, "Succession and goose herbivory in monsoonal wetlands of the Keoladeo National Park, Bharatpur, India", uses a succession model developed for midwestern prairie potholes of the U.S. (van der Valk 1981) to build a succession model for monsoonal wetlands based on the first two papers and additional evidence from vegetation surveys, observations on sites recovering from goose grazing, and seedbank studies.

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SECTION 1. THE FOOD HABITS OF GREYLAG AND BARHEADED GEESE IN THE KEOLADEO NATIONAL PARK, INDIA

The food habits of Greylag and Barheaded Geese in the Keoladeo National Park, India

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INTRODUCTION

More than 6,000 geese overwinter in the Keoladeo National Park, Bharatpur, Rajasthan, India (Fig. 1). The Eastern Greylag Goose (Owen 1980, Johnsgard 1978) is the most common goose. At its peak, the Greylag Goose population consists of about 5000 birds. They arrive in the Park by early November and leave by mid-March, a pattern which is typical of northern India (Ali and Ripley 1968). The Barheaded Goose, at between 500-1000 individuals, is less numerous. Barheaded Geese arrive in numbers by late December and leave by mid-April. This goose has undergone significant population decline in the past several decades (Gole 1982).

The food habits of Greylag and Barheaded Geese have never been quantified for any part of their overwintering grounds on the subcontinent of India. Some factors contributing to seasonal food selection (i.e., availability versus physiological needs for migration and breeding) will be explored.

It was not possible to kill geese because we were working in a national park, so fecal analysis was used, a method which enables the population to be resampled throughout the season (Storr 1961, Stewart 1967). Geese digest relatively little compared to other vertebrate herbivores (Mattocks

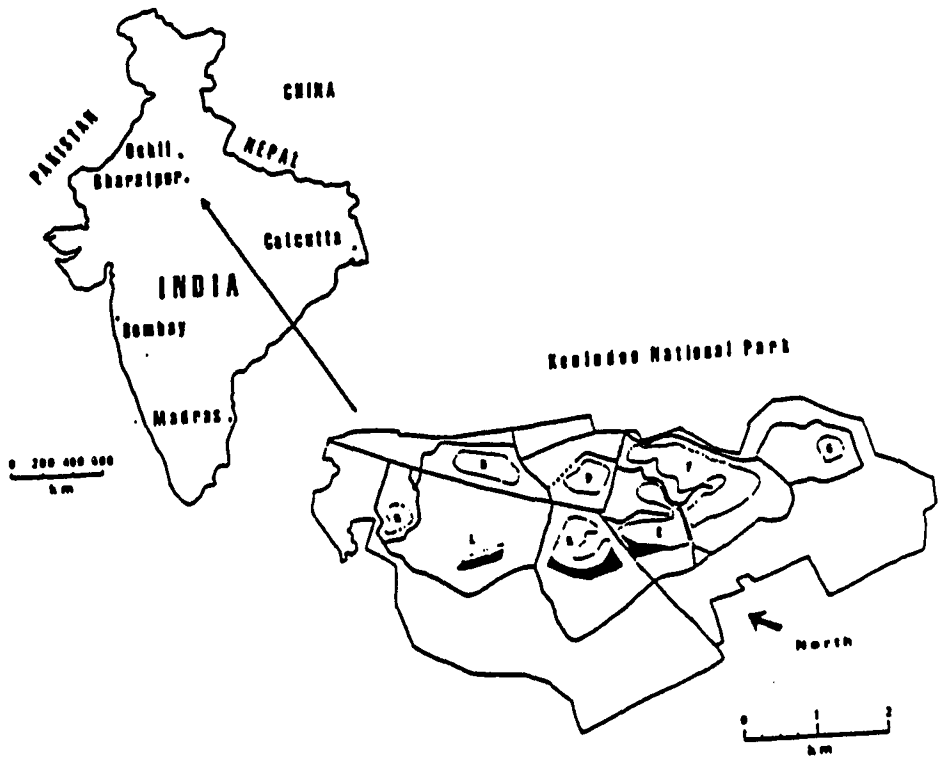

Fig. 1. Location of study site, Keoladeo National Park, Bharatpur, Rajasthan, India (upper left). Areas grazed by goose flocks of more than 100 birds, November 1985 to April 1986 (lower right). Shaded are Greylag Goose areas, darkened are Barheaded areas abandoned by Greylag Geese. Letters correspond to area (block) names

1971, Owen 1975) making them good candidates for fecal analysis. They digest about 28% of the cellulose and 25% of the hemicelluloses in their diets (Buchsbaum et al. 1986). Undigested food can pass through a goose in as little as one hour (Ebbinge et al. 1975, Dorozynska 1962). Thus, it seems that the food habits of geese can be described adequately through fecal analysis.

METHODS

Study Site

The Keoladeo National Park near Bharatpur, India (27° N Lat., 70° 32'E; 50 km west of Agra) lies in the floodplain of the Gambhir and Banganga Rivers (Fig. 1). While this wetland lies in a natural depression, each year the water depth is enhanced by adding rainwater through a floodgate from a reservoir, the Ajun Bund. The Park is now under the control of the State Government of Rajasthan Forestry Department. Prior to 1973 when it was declared a wildlife sanctuary, the area was used as the Maharajah of Bharatpur's private shooting reserve (Ali and Vijayan 1986).

Water levels in this wetland fluctuate both within and between years. After the monsoon (June to September), water levels are at their annual maximum. As the monsoon waters recede during the fall and winter, parts or all of a monsoonal wetland may become dry (Gopal 1973). After a poor monsoon, the whole wetland may be dry for the entire year. In a very heavy monsoon year, the water may be more than two metres deep, with most of the Park's 29 km^2 area inundated with water for at least one month.

This wetland is dominated by one species of grass, Paspalum distichum (Maheshwari 1963). This became much more prevalent in the wetland after the banning of cattle grazing in 1981 (Ali and Vijayan 1986). Only the deepest parts of the wetland are free of this grass; they are dominated by submersed plant species such as *Potamogeton indicus* and *Hydrilla verticillata*. Savanna areas which tend to be flooded for short periods of time after a heavy monsoon are dominated by the tall grass species, *Vetiveria zizanioides*, with occasional trees, primarily *Acacia nilotica*. Geese, most typically found in the *Paspalum distichum* dominated areas, also have been observed in all these vegetation types in Bharatpur. In *Vetiveria zizanioides* stands, geese may be found in the wetter depressions that are free of tall grasses.

Field Collection of Droppings

Typically, the two goose species preferred to graze in separate but adjacent flocks in a single area (Fig. 1). Goose droppings were collected every month from wherever goose flocks were currently grazing. To ensure a good sampling over the goose population, 100 fresh droppings were collected over a wide area in a given location. Greylag Goose droppings were distinguished from those of Barheaded Geese according to size, color, texture and location. The 100 droppings were carried to the lab, carefully cleaned of debris, and then mixed. This composite sample was homogenized with water in an electric blender on the same day that it was collected in the field. Homogenization improved the quality of the slides by clearing dark pigments from the material. After mixing for one minute, the material was washed for about five minutes through a 0.1 mm (200 mesh) screen until thoroughly cleaned. This cleaned material retained in the screen was dried in an oven at 72^{o} C for future slide preparation or immediately mounted on slides (Scott and Dahl 1980).

Five duplicate slides were prepared for each monthly composite sample (n) following a method described by Baumgartner and Martin (1939). A small amount of fecal material was boiled in a drop of Hertwig's solution over a burner. Next, a few drops of Hoyer's mounting medium were put on the boiled material, heated and covered with a 22 x 50 mm cover slip while still hot. The material was spread evenly over the slide to minimize fragment overlap. Completed slides were then dried at room temperature or at 55^{o} C in a drying oven. This method does not work during humid weather conditions due to the hygroscopic nature of the mounting medium.

A reference plant collection for the purpose of identifying fecal fragments was constructed. Samples of known plant species were first chopped, then ground in a blender followed by the same cleaning and mounting methods used for the fecal material. Because leaves, stems, seeds, and roots are readily distinguishable from each other, a reference slide was made for each plant part. Certain species changed slightly in microscopic appearance during the season (e.g., trichomes in Paspalum distichum) so seasonal slides were prepared as necessary.

Slide reading followed that described by Scott and Dahl (1980). Starting at the upper left hand corner of the slide, each fragment was recorded in a field where three identifiable fragments occurred until 50 fields had been read. From this information, per slide percentages were obtained. For both goose species, five duplicate slides were read and averaged for each monthly composite, in each goose grazing location with more than 100 geese. The components of variance for the means of the plant fragments in the goose diet were analyzed using the Proc Varcomp option in SAS (Statistical Analysis System 1985).

The method provides estimates in terms of surface area only. Since the relationship between area and volume or weight varies widely among plant parts, the results give only an approximate measure of the contribution of the various plants to the diet.

RESULTS

Greylag Goose Diet

The main source of variation in food habits is from the month collected rather than goose feeding location or duplicate slides (Table 1). Seasonal diet differences are apparent. Early in the overwintering season, seeds are common in the diet of Greylag Geese. Seed ripening occurs for many plants during the postmonsoon conditions of November and December, and seeds made up 64.7% of the diet in these months. Most of these seeds are from *Nymphaea nouchali*, *Oryza rufipogon*, *Nymphoides cristatum*, and *Paspalum distichum* (Table 2). When seeds become scarce, (they contributed only 1.5% in January and less subsequently), grasses increase in importance in the diet, to form almost all of the diet (Fig. 2) from January until migration. Most of the grass contribution comes from the stems and leaves of one species, *Paspalum distichum*, 68% over the entire season. In all, at least 21 plant species are eaten by Greylag Geese, with additional, minor contributions from insects and snails (Table 2).

Barheaded Goose Diet

Striking differences are seen for Barheaded Geese in their seasonal eating patterns (Fig. 2). Grasses are

Table 1. Components of variance of selected plant species in the diets of Greylag and Barheaded Geese

	Variance Component Estimate			
Plant	Month	Area	Sample	Total Variance Component
GREYLAG GOOSE				
Paspalum distichum	598.3	130.2	12.2	740.7
Nymphaea nouchali	180.2	32.5	7.0	219.7
Oryza rufipogon	293.6	76.9	7.5	378.0
BARHEADED GOOSE				
Paspalum distichum	1434.2	20.0	8.7	1462.9
Pisum sativum	939.7	6.7	13.7	960.1

Table 2. Food habits of the Greylag Goose, Keoladeo National Park, Bharatpur, India (November 1985 to March 1986). Averages for all plant species in diet, given by percent

PLANT	MONTH November	December	January	February	March	Average
Paspalum distichum	29.4	31.2	90.0	92.2	96.1	67.8
leaves	(8.4)	(1.9)	(33.4)	(11.7)	(13.5)	(13.8)
stems	(8.4)	(17.3)	(55.5)	(80.4)	(82.2)	(48.7)
seeds	(12.6)	(11.9)	(1.1)	(0.2)	(0.4)	(5.2)
Nymphaea nouchali	55.1	9.4	0.1	0.0	0.0	12.9
leaves	(3.0)	(0.8)	0.0	0.0	0.0	(0.8)
seeds	(52.1)	(8.6)	<0.1	0.0	0.0	(12.1)
Oryza rufipogon	1.2	46.7	2.3	0.9	0.8	10.4
leaves	(1.2)	(11.6)	(2.1)	(0.9)	(0.8)	(3.3)
seeds	0.0	(35.1)	(0.2)	0.0	(0.1)	(7.1)
Ipomoea aquatica	1.2	0.9	0.9	2.8	0.5	1.3
leaves	(1.2)	(0.8)	(0.9)	(2.8)	(0.5)	(1.2)
seeds	0.0	(0.1)	0.0	0.0	0.0	(0.1)
Sagittaria guayanensis	2.4	2.5	<0.1	0.0	0.0	1.0
leaves	(2.4)	(1.8)	(<0.1)	0.0	0.0	(0.8)
seeds	0.0	(0.7)	0.0	0.0	0.0	(0.1)

Table 2. (Continued)

PLANT	MONTH November	December	January	February	March	Average
insect and snails	3.0	5.3	0.6	0.7	0.9	2.1
seeds (general)	(64.7)	(58.4)	(1.5)	(0.3)	(0.6)	(25.1)
Nymphoides cristatum	7.8	1.7	0.1	<0.1	0.1	1.9
leaves	(7.8)	(0.3)	0.0	0.0	0.0	(1.6)
seeds	0.0	(1.5)	(0.1)	(<0.1)	(0.1)	(0.3)
Scirpus tuberosus	0.0	0.7	0.5	0.4	0.1	0.3
Cynodon dactylon	0.0	0.5	0.5	0.1	0.1	0.2
Panicum paludosum (stem)	0.0	0.5	1.7	1.1	0.6	0.8
grass seed	0.0	0.3	0.0	0.0	0.0	0.1
Paspalidium flavidum	0.0	0.2	0.5	0.6	0.3	0.3
Sporobolus sp.	0.0	0.1	0.8	0.1	0.3	0.2
herbaceous seed	0.0	0.1	0.0	0.0	0.0	<0.1
Hemiadelphus polyspermus	0.0	0.1	<0.1	0.1	<0.1	<0.1
Scirpus littoralis	0.0	0.0	1.4	0.4	<0.1	0.4

Table 2. (Continued)

PLANT	November	December	January	February	March	Average
	MONTH					
Eleocharis palustris	0.0	0.0	0.3	0.1	0.1	0.1
Utricularia sp.	0.0	0.0	0.1	0.1	0.0	<0.1
Ceratophyllum demersum	0.0	0.0	<0.1	0.1	0.0	<0.1
Cyperus alopecuroides	0.0	0.0	0.3	<0.1	0.0	0.1
grass stem	0.0	0.0	0.0	0.0	<0.1	<0.1
Total	100.1	100.2	100.2	99.7	99.9	100.0

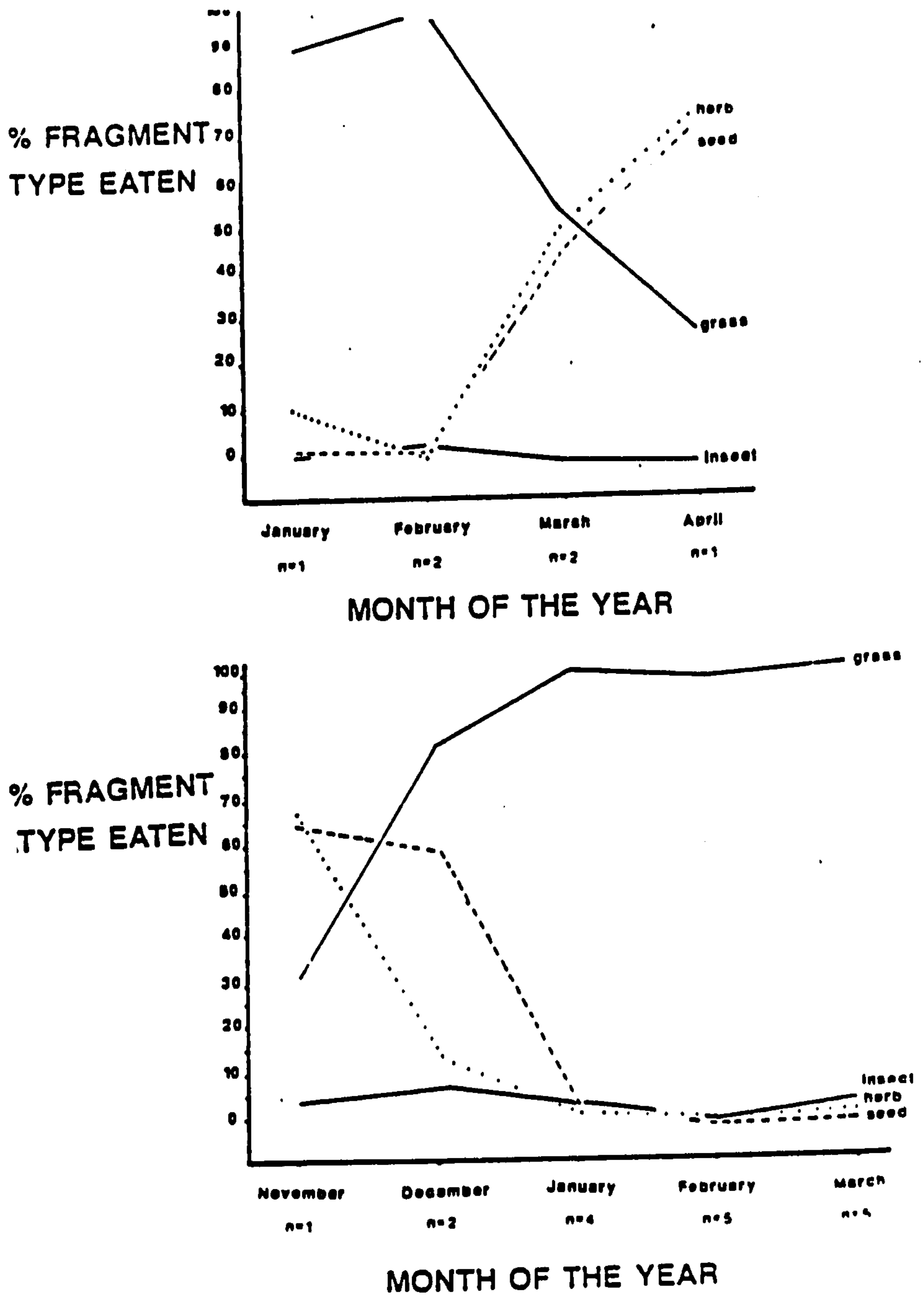

Fig. 2. Monthly comparison of fragment type in the feces of Greylag (bottom) and Barheaded Geese (top), November 1985 to March 86, in the Keoladeo National Park, Bharatpur, India. Number of composite samples from goose flocks is 'n'

important in January and February but drop sharply in March and April when herbaceous plants and seeds become important. In January, the main constituent of the diet is wheat (Table 3). In February, when field crops are not available, native Paspalum distichum predominates. Overall, Paspalum distichum leaves comprise 45% of the overwintering diet. By March and April, once again the diet is mostly field crops, but chiefly of peas (Pisum sativum) and grams (Cicer arietinum) instead of wheat. Barheaded Geese utilized a total of 21 different plant species, 3 of which were of agricultural origin. Insects and snails constitute a very low percentage of the diet throughout the season (Table 3).

Barheaded Geese were thus less dependent on native wetland plants and only in February did these comprise all of their diet, 95% of it being Paspalum distichum. In parts of the season, Barheaded Geese relied on agricultural crops (Table 3). Overall, they utilized 52% wild plants in their diet whereas Greylag Geese used only wild plants.

Table 3. Food habits of the Barheaded Goose, Keoladeo National Park, Bharatpur, India (January 1986 to April 1986). Averages for all plant species in diet, given by percent

	MONTH				
PLANT	January	February	March	April	Average
Paspalum distichum	10.8	95.0	49.5	26.4	45.4
leaves	(10.8)	(94.9)	(49.5)	(26.4)	(45.3)
stems	0.0	0.0	0.0	0.0	0.0
seeds	0.0	(0.1)	0.0	0.0	< 0.1
Pisum sativum	4.6	0.0	44.5	72.3	30.2
seed	0.0	0.0	(42.2)	(72.1)	(28.5)
stems and leaves	(4.6)	0.0	(2.3)	(0.2)	(1.8)
Cicer arietinum	3.1	0.0	2.7	0.6	1.6
seed	0.0	0.0	(0.1)	(0.6)	(0.2)
stems and leaves	(3.1)	0.0	(2.6)	0.0	(1.4)
Triticum aestivum	65.1	0.0	0.0	0.0	16.3
seeds (general)	(0.7)	(0.1)	(41.9)	(73.3)	(29.0)
insect and snails	0.0	2.2	0.3	0.1	0.7
Cynodon dactylon	5.5	0.7	1.5	0.3	2.0

Table 3. (Continued)

PLANT	MONTH January	February	March	April	Average
Ipomoea aquatica (leaves)	0.8	0.2	0.1	0.0	0.3
Paspalidium flavidum	2.0	0.4	0.6	0.0	0.8
Panicum paludosum	2.1	0.3	0.6	0.0	0.8
Ceratophyllum demersum	0.0	0.3	0.0	0.0	0.1
Sporobolus sp.	1.4	0.2	0.0	0.2	0.5
Scirpus tuberosus	2.6	0.4	0.3	0.0	0.8
Nymphoides cristatum	0.2	0.1	0.0	0.0	0.1
Scirpus sp.	0.0	0.2	0.0	0.0	<0.1
Sagittaria guayanensis (leaves)	0.2	0.1	0.0	0.0	0.1
Scirpus littoralis	0.0	0.0	0.1	0.0	<0.1
Eleocharis palustris	0.0	0.0	0.0	0.1	<0.1

Table 3. (Continued)

PLANT	MONTH January	February	March	April	Average
Utricularia sp.	0.5	0.0	0.0	0.0	0.1
Hemiadelphus polyspermus	0.2	0.0	0.0	0.0	<0.1
Nymphaea nouchali (seed)	0.2	0.0	0.0	0.0	<0.1
herbaceous leaf	0.4	0.0	0.0	0.0	0.1
Total	99.7	100.0	99.7	100.0	99.9

DISCUSSION

Geese feed on a wide variety of plants (McFarland and George 1966, Pollard and Walters-Davies 1968, Owen and Kerbes 1971, Owen 1976, Burton et al. 1979, Prevett et al. 1979, Summers and Grieve 1982). The particular species of plants consumed depends on the flock's geographic location and on plant availability.

In the Keoladeo National Park, India, Barheaded Geese eat more gramineous leaves than they are reported to elsewhere (Table 3; Fig. 2). In their nesting range in the Soviet Union, they feed mostly on terrestrial vegetation, including the seeds of grasses and legumes; in tidal areas Barheaded Geese eat seaweeds, crustaceans and invertebrates (Dement'ev and Gladkov 1968).

Greylag Geese in the Keoladeo National Park eat seeds early in the overwintering season and grass parts in later months, not greatly different from the reported diet of the Eastern Greylag Goose in the Soviet Union (Table 2; Fig. 2). Dement'ev and Gladkov (1968) reported that Greylag Geese eat grasses of various sorts (winter rye, hair grasses, awnless broom grass, Leerzia sp.), the fruits of Potamogeton pectinatus and the seeds of Polygonum sp. and oats. In the Netherlands (Loosjes 1974) and in Spain (Amat 1986), Greylag Geese eat a wild plant diet of mostly Scirpus lacustris root pieces and the tubers or rhizomes of Scirpus maritimus. Western Greylag Geese, Anser anser anser, in Scotland eat mainly grasses but in late summer switch to ripening oats (Newton and Kerbes 1974). In the winter, they primarily feed in agricultural fields where they eat oat and barley seeds, later switching to potato crops (Newton and Campbell 1973, Newton et al. 1974).

Greylag Geese in the Keoladeo National Park have very different food habits from the Barheaded Geese grazing in the same area. Large-billed geese such as the former are adapted for rooting, whereas smaller-billed geese such as the latter may be better suited for grazing on shorter grasses (Reed 1976) in shallower water. Other studies have demonstrated that goose species in one area may have very different food habits due to differences in food preference (Craven 1984) as well as morphological differences (Reed 1976).

The Greylag Geese maintain themselves on the nearly apple-sized fruits of Nymphaea nouchali (and many kinds of seeds) in the early part of their overwintering season (Table 2). Later in the season, they can be observed forcibly pulling up whole culms of Paspalum distichum which may be growing in water approaching 2 metres deep. Barheaded Geese, which have a much smaller bill, tend to tear off the leaves of grasses rather than tackle the bulky stems (Table 3). They can often be seen grazing in shallow areas abandoned by Greylag Geese, perhaps preferring the shorter forage provided (Fig. 1).

Barheaded Geese spend most of their time grazing in agricultural fields during certain parts of the winter season, but, during the day, they also graze on wild grasses in the wetland. Since more than half of their diet comes from a wild food source (Table 3), they cannot be thought of as completely dependent on agriculture.

It is not known whether Paspalum distichum was an important food item in the diet of geese prior to this plant's spread after the cessation of cattle grazing in 1981. It is clear from this study that it is now an important component of the diet for both goose species overwintering in the Keoladeo National Park (Tables 2 and 3). Studies now in progress will explore the role of geese in creating openings in this nearly monospecific grass cover.

To some extent, seasonal dietary requirements of geese dictate their choice of food (Ydenberg and Prins 1981, Halse 1984, Hobaugh 1985). These authors suggest that geese choose more high energy food prior to migration or breeding to accumulate fat reserves. In India, Barheaded Geese behave in this fashion, in that, prior to migrating to their Himalayan breeding grounds, they eat foods such as peas, grams and, a little earlier in the season, young wheat which are likely to have a good amino acid profile, but then, these plants are only available during this time. During February, between the seasons of ripening legumes and young wheat, the geese return to graze exclusively in the wetland.

For Greylag Geese, one cannot make a case for food selection on their overwintering grounds based on migration or breeding requirements. Shortly after the Greylag Geese arrive for their five month sojourn, they choose to eat the energy-rich seeds available during the post-monsoon period (*Nymphaea nouchali*, *Oryza rufipogon*). Just before migrating from India, they switch to grasses when seeds are no longer available. For Greylag Geese, and to some extent Barheaded Geese, availability seems to be a major determinant of their seasonal food selection.

SUMMARY

The food habits of overwintering Greylag (*Anser anser rubrirostris*) and Barheaded (*Anser indicus*) Geese are discussed for the Keoladeo National Park, Bharatpur, India. Greylag Geese eat mostly seeds of *Nymphaea nouchali* and *Oryza rufipogon* in November and December but shift to native grasses such as *Paspalum distichum* in January. They eat mostly *Paspalum distichum* until they leave in March. Barheaded Geese eat mostly young wheat (*Triticum aestivum*) in January, native grasses, such as *Paspalum distichum* in February and change to field peas (*Pisum sativum*) and grams (*Cicer arietinum*) in March and April. Overall, *Paspalum distichum* is the most important species in the diet of these geese, comprising 67.8% of the Greylag Goose and 45.4% of the Barheaded Goose diet.

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SECTION 2. EFFECT OF WATER DEPTH AND CLIPPING FREQUENCY ON THE GROWTH AND SURVIVAL OF FOUR WETLAND PLANT SPECIES

Effect of water depth and clipping frequency on the growth and survival of four wetland plant species

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ABSTRACT

In an garden study conducted in north-central India, four plant species were either clipped weekly, clipped every two weeks, or left unclipped while growing at one of 3 water levels (0 cm, 3 cm, or 13 cm below the surface of the water). When clipped underwater, individuals of _Ipomoea aquatica_ Forsk., _Paspalidium punctatum_ A. Camus, and _Paspalum distichum_ Linn. usually died but those of _Nymphoides cristatum_ Kuntze did not. In a companion field study in a monsoonal wetland in the Keoladeo National Park, plants of _Ipomoea aquatica_ and _Paspalum distichum_, the only species tested, also usually died when clipped underwater.

In the garden study, the total biomass of clipped plants, including above- and below-ground biomass, depended on both water depth and clipping frequency. Most species had less total biomass when clipped than unclipped. For example, plants of _Paspalum distichum_ that were clipped every two weeks had less total biomass (5.4 g) than unclipped plants (9.5 g) in 0 cm of water. An exception, the total biomass of unclipped plants of _Nymphoides cristatum_ (1.8 g), did not differ significantly from plants clipped every week and every two weeks in -3 cm water (1.1 and 1.4 g, respectively). In general, clipping reduced mean root mass and increased mean shoot mass.

Herbivores, such as geese, seem to create openings in emergent wetland vegetation of monsoonal wetlands in India, as a result of the inability of certain plants to survive and/or grow after being grazed underwater.

INTRODUCTION

A distinctive feature of grazing in wetlands is openings in the emergent vegetation. Goose grazing on the Gulf Coast of the United States creates "eatouts" (Lynch et al. 1947) and at La Perouse Bay, Canada, causes openings and depressions in the surface of the wetland (Jeffries et al. 1979). In the midwestern United States, muskrats can destroy most of the emergent vegetation in prairie glacial wetlands and transform them temporarily into small lakes (Weller 1978). In the monsoonal wetland of the Keoladeo National Park, India, I have seen openings appear in the emergent vegetation in areas where geese have been grazing (Middleton 1989).

Although there are many terrestrial studies of the effect of clipping on the growth of plants, terrestrial studies cannot be directly applied to wetland situations. Aquatic plants are rooted in an anoxic environment, and their roots and rhizomes are supplied with O_2 through a series of more or less integrated air spaces connecting leaves to roots (Laing 1940, Sculthorpe 1967, Hutchinson 1975, Armstrong 1978, Etherington 1983, Mitsch and Gosselink 1986). In the case of rice, O_2 moves along the outside of the plant from exposed leaves in a continuous film between the stem and water (Raskin and Kende 1985). Clipping the upper portion of emergent plants could interfere with O_2 supply to roots and rhizomes and cause the death of the plant. Summer cutting of *Typha angustifolia* has been used in Czechoslovakia to maintain large areas of open water in fish ponds (Husak 1978). In Michigan, cutting *Typha latifolia* and *Typha angustifolia* underwater resulted in anaerobic respiration and the production of ethanol in roots. If part of the plant was left above water, the plant was able to continue aerobic respiration (Sale and Wetzel 1983). In an Indian study, if the cut stubble of *Typha angustata* was submersed for two weeks, the plants died (Singh et al. 1976). Terrestrial plants, however, generally do not die when they are clipped, in part because there is sufficient O_2 present in the soil pore spaces for respiration.

The effect of herbivory or clipping on net primary productivity has been little studied in aquatic plants but their general responses to herbivory, short of death, should be similar to that of terrestrial species: (1) herbivory may reduce the growth and reproduction of the plant; (2) there may be no overall change in the growth or reproduction of the plant; (3) low levels of herbivory may increase the growth and reproduction of the plant because the plant can overcompensate for losses incurred by herbivory (McNaughton 1983). There is evidence that moderate to low amounts of grazing may have the effect of increasing the primary production of terrestrial grasslands (McNaughton 1979, Dyer et al. 1982, Hilbert et al. 1981) and the production of aquatic waterlilies grazed by beetles (Wallace and O'Hop 1985). In studies suggesting compensatory growth of clipped plants, however, there is seldom an adjustment for root loss due to shoot regrowth in the calculation of overall growth after herbivory (Belsky 1986).

I tested the hypothesis that underwater grazing kills aquatic plants. If my hypothesis is correct, the grazing of plants creates the open water patches that I observed in the wetlands of the Keoladeo National Park. The four plant species chosen for this study all are eaten by geese, as determined through microhistological examination of droppings of Greylag and Barheaded Geese (Middleton and van der Valk 1987).

STUDY AREA

Both studies were carried out in or near the Keoladeo National Park in Bharatpur, Rajasthan (27^{o} 13'N Lat., 77^{o} 32'E) during periods corresponding to the goose overwintering period in northern India (October - March). In an Indian monsoonal wetland, the annual maximum water depth of up to 2 m depends on the amount of rainfall received from June to October, the monsoon period. Water depth then declines, and the area covered with water recedes slowly during the winter (minimum temperatures can reach 2^{o} C) and rapidly during the summer months preceding the next monsoon (maximum temperatures can reach 50^{o} C).

EXPERIMENTAL DESIGN

Garden Study

After the cessation of water buffalo grazing in the Park in 1981, Paspalum distichum became the dominant emergent grass (Ali and Vijayan 1986). Paspalidium punctatum (Maheshwari 1963) is an emergent grass restricted to shallower water depths than Paspalum distichum. The dominant herb, Ipomoea aquatica, and an anchored floating-leaved species, Nymphoides cristatum, are found throughout the area dominated by Paspalum distichum.

Plants were grown either from seed (Paspalidium punctatum and Nymphoides cristatum) or from cuttings of less than 10 cm in height (Ipomoea aquatica and Paspalum distichum) in 20 cm diameter pots for two months under moist soil conditions (0 cm water), except for plants of Nymphoides cristatum which were submersed, so that there was 13 cm of water above the surface of the soil (-13 cm). All plants were fertilized with goose droppings every three weeks. Every month, plants were dusted with an insecticide to control insect herbivory. The garden study was conducted during November 1985 - March 1986 in a garden near the Keoladeo National Park.

A factorial, split-plot, experimental design was used, with the main plot being water depth, split among clipping treatments. There were 18 main plots (trays) with six assigned randomly to a water depth treatment. The soil surface in a pot was either 0, -3, or -13 cm below the water surface. Within a tray, there were three pots of each species, each randomly assigned to one clipping treatment: unclipped, clipped every two weeks (biweekly), or clipped weekly. There were 6 replicates of each clipping X water depth treatment, with each replicate in a different tray.

To simulate the action of goose grazing, each plant was clipped by pulling the plant upward while it was being snipped near the soil surface with a pair of scissors. Each week, clipped shoots were oven dried and weighed. At the end of the twenty-first week of the experiment, whole plants were harvested, separated into roots and shoots, dried, and weighed.

After a plant appeared dead, it was monitored throughout the remainder of the experiment for new shoots. If no new shoots emerged, the plant was considered to have died at the time it was first recorded as dead.

Field Study

This study was conducted in the monsoonal wetland of the Keoladeo National Park during the winter season from December 1986 - February 1987, a year after the garden study. The two species examined, *Paspalum distichum* and *Ipomoea aquatica*, also had been used in the garden study.

Four areas were selected in the Park at random with standing water of 30-45 cm depth. In each area, ten points were randomly chosen along a linear transect. At each point, the two nearest plants of each species rooted in the soil closest to the point were selected. One plant was randomly chosen to be clipped and the other left as a control (unclipped). All culms originating from the rooting point of a plants were clipped at soil level only in the beginning of the experiment. Each plant was revisited every two weeks to determine if it was alive or dead, and if any new shoots had grown.

Calculations

Total biomass is the shoot mass of all clippings in the experiment plus the root mass at the end of the experiment. The effect of clipping and water depth on total biomass, shoot mass and root mass was determined using a two-way Analysis of Variance (ANOVA). Significant differences among mean total biomass were determined using Least Significant Differences (LSD; SAS 1982; Cochran and Cox 1957) because there was no significant interblock effect for total biomass.

Survivorship was compared between treatment combinations using failure time analysis based on daily survival rates ($\hat{s}_i$; Heisey and Fuller 1985):

$$\hat{s}_i = \frac{x_i - y_i}{x_i}$$

where x_i is the number of days alive at the end of the interval (i), and y_i is the number of deaths in the interval. With weekly observations, it was not possible to determine on which day of the week a plant had died, so if a plant died, its death was assigned to day 3.5.

To plot a survivorship curve, interval (weekly or biweekly) survival rates ($\hat{S}i$) were calculated as

$$\hat{S}_i = \hat{s}_i^{L_i}$$

where L_i = length of interval, i.e., 7 days for the garden study and 14 days for the field study (Heisey and Fuller 1985).

Span survival rates ($\hat{S}^*$) are the product of the interval survival rates,

$$\hat{S}^* = \prod_{t=1}^{21} \hat{S}i .$$

An $\hat{S}^*$ = 1.0 indicates that all plants lived throughout the entire experiment, while $\hat{S}^*$ = 0 indicates that all plants died sometime before the last interval of the experiment.

RESULTS

ANOVAs for total biomass, shoot mass and root mass for each species are given in Table 1. Only significant differences are discussed.

Ipomoea aquatica

In the garden study, clipped plants began to die after 4-10 weeks when cut underwater, (S^* = 0.09-0.16; Table 2; Fig. 1), but clipped plants grown in 0 cm water generally survived (S^* = 0.83). All unclipped plants survived at all water depths (S^* = 1.00; Table 2). In the field study, plants clipped underwater had much lower survivorship (S^* = 0.09) than unclipped plants (S^* = 0.97; Table 3; Fig. 1).

Total mass for unclipped plants in 0 cm of water was more than twice that of any other treatment (6.3 g; Table 4) but decreased with water depth (Table 1). In 0 cm of water, clipping reduced the total biomass (Tables 1 and 4). Root mass was highest in unclipped plants grown in 0 cm of water (5.5 g) and decreased with clipping and water depth. Shoot mass was lowest in unclipped treatments in 0, -3 and -13 cm of water (0.8, 0.4, and 0.7 g, respectively; Table 4).

Table 1. ANOVAs for total biomass (g), root mass (g), and shoot mass (g) for four species of wetland plants subjected to various levels of clipping and water depth. '*' indicates significance at a 95% or greater level. The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 - March 1986)

Variable	Ipomoea F ratio	Nymphoides F ratio	Paspalum F ratio	Paspalidium F ratio
Total Biomass				
block	0.5	0.4	0.8	0.7
depth	13.7*	12.4*	0.1	3.7
clipping	12.9*	5.1*	16.1*	77.6*
depth x clip	2.0	4.3*	0.6	1.6
Root Mass				
block	0.4	1.6	4.4*	0.7
depth	17.7*	9.3*	24.5*	8.8*
clipping	56.5*	17.7*	48.2*	162.3*
depth x clip	7.1*	7.7*	11.4*	11.4*
Shoot Mass				
block	0.6	1.0	1.3	1.1
depth	3.0	8.5*	1.1	0.4
clipping	7.2*	26.0*	3.7*	1.0
depth x clip	1.4	1.0	2.1	5.7*

Table 2. Span survival rates ($\hat{S}^*$) for four species of East Indian aquatic plants at 3 water depths, 0 cm, -3 cm, and -13 cm, and three clipping levels, unclipped, biweekly (every two weeks) at soil level, and every week at soil level. The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 to March 1986

		Water Depth (cm)		
Species	Clipping Level	0	-3	-13
Ipomoea	unclipped	1.00	1.00	1.00
	biweekly	0.83	0.09	0.16
	weekly	0.83	0.09	0.11
Nymphoides	unclipped	0.31	1.00	1.00
	biweekly	0.17	1.00	1.00
	weekly	0.68	1.00	0.83
Paspalum	unclipped	1.00	1.00	1.00
	biweekly	1.00	0.33	0.17
	weekly	0.00	0.01	0.49
Paspalidium	unclipped	1.00	1.00	0.83
	biweekly	1.00	0.16	0.03
	weekly	0.16	0.01	0.01

Table 3. Span survival rates ($\hat{S}^{*}$) for field study of *Ipomoea aquatica* and *Paspalum distichum* conducted in the Keoladeo National Park from December 1986-February 1987

	Clipping Level	
Species	unclipped	clipped
Ipomoea	0.97	0.09
Paspalum	1.00	0.45

Fig. 1. Survivorship curves for four species of aquatic plants in the garden study over a 21 week experiment. Based on daily survival rates in three water depths (0 cm, -3 cm, -13 cm) and three clipping intensities (unclipped, every two weeks (biweekly) at soil level, and weekly at soil level). The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 to March 1986

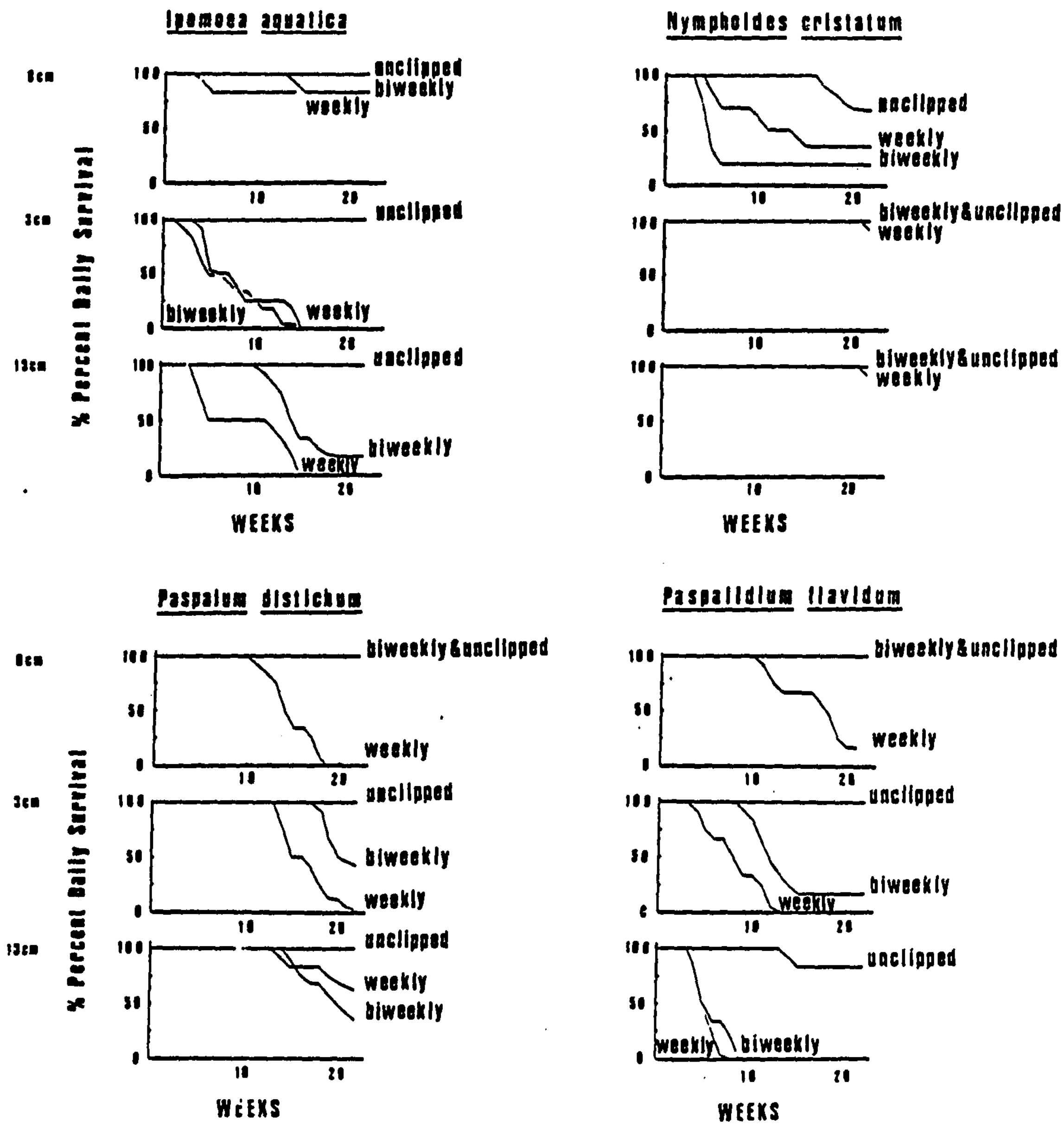

Ipomoea aquatica
Nymphoides cristatum
Paspalum distichum
Paspalidium flavidum
% Percent Daily Survival
0cm
3cm
13cm
unclipped
biweekly
weekly
biweekly&unclipped
WEEKS
100
50
0
10
20

Table 4. Ipomoea aquatica. Means (X) and standard errors (S.E.) of total biomass (g), root mass (g), and shoot mass (g) at 3 water depths, 0 cm, -3 cm, and -13 cm, and three clipping levels, unclipped (C), biweekly (B; every two weeks) at soil level, and every week (W) at soil level. Means for total biomass of clipped plants that differ significantly from controls by LSD analysis are indicated by a '*'. The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 to March 1986

		Water Depth (cm)					
		0		-3		-13	
		X	S.E.	X	S.E.	X	S.E.
	total biomass	6.3	+/- 0.1	3.1	+/- 0.1	2.3	+/- 0.2
C	root mass	5.5	+/- 0.5	2.8	+/- 0.8	1.5	+/- 0.4
	shoot mass	0.8	+/- 0.1	0.4	+/- 0.1	0.7	+/- 0.2
	total biomass	3.0	+/- 0.5*	2.0	+/- 0.3	1.1	+/- 0.2
B	root mass	1.1	+/- 0.1	0.5	+/- 0.2	0.3	+/- 0.1
	shoot mass	1.9	+/- 0.5	1.5	+/- 0.3	0.8	+/- 0.2
	total biomass	2.6	+/- 0.3*	1.8	+/- 0.5	1.2	+/- 0.2
W	root mass	0.9	+/- 0.2	0.2	+/- 0.1	0.3	+/- 0.2
	shoot mass	1.8	+/- 0.3	1.6	+/- 0.5	0.9	+/- 0.2

Nymphoides cristatum

In the garden study, all plants grown underwater, whether clipped or unclipped had high survivorship ($\hat{S}^*$ = 0.83 Fig. 1), but not in 0 cm water ($\hat{S}^*$ = 0.17-0.68; Table 2; Fig. 1).

In unclipped plants, total biomass increased with water depth (Tables 1 and 5) with the highest total biomass in -13 cm of water (4.4 g; Table 5). Total biomass was lower in plants clipped weekly and every other week in -13 cm of water (2.2 and 1.9 g, respectively; Table 5). The largest contribution to total biomass was root mass in unclipped plants; root mass increased with water depth (0.7, 1.7, and 4.1 g, respectively; Table 5). Most of the total biomass of clipped treatments was contributed by shoot mass (Table 5).

Paspalum distichum

In the garden study, clipped plants had lower survivorship in submersed treatments, beginning in week 12 of the experiment ($\hat{S}^*$ = 0.01-0.49), as did weekly clipped plants in 0 cm water ($\hat{S}^*$ = 0.00; Table 2; Fig. 1). In contrast, all unclipped plants at all water depths, and plants clipped every two weeks in 0 cm water, survived ($\hat{S}^*$ = 1.00; Table 2; Fig. 1). In the field study, clipped plants had lower survivorship ($\hat{S}^*$ = 0.45) than unclipped plants ($\hat{S}^*$ = 1.00; Table 3).

Table 5. *Nymphoides cristatum*. Means (X) and standard errors (S.E.) of total biomass (g), root mass (g), and shoot mass (g) at 3 water depths, 0 cm, -3 cm, and -13 cm, and 3 clipping levels, unclipped (C), biweekly (B; every two weeks) at soil level, and every week (W) at soil level. Means for total biomass of clipped plants that differ significantly from controls by LSD analysis are indicated by a '*'. The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 to March 1986

		Water Depth (cm)					
		0		-3		-13	
		X	S.E.	X	S.E.	X	S.E.
	total biomass	0.7	+/- 0.1	1.8	+/- 0.1	4.4	+/- 0.1
C	root mass	0.7	+/- 0.2	1.7	+/- 0.3	4.1	+/- 0.8
	shoot mass	0.1	+/- 0.1	0.1	+/- 0.1	0.3	+/- 0.1
	total biomass	1.4	+/- 0.1	1.4	+/- 0.2	2.2	+/- 0.3*
B	root mass	0.8	+/- 0.2	0.9	+/- 0.1	0.8	+/- 0.3
	shoot mass	0.6	+/- 0.1	0.6	+/- 0.2	1.4	+/- 0.3
	total biomass	0.9	+/- 0.1	1.1	+/- 0.1	1.9	+/- 0.2*
W	root mass	0.6	+/- 0.2	0.5	+/- 0.1	0.9	+/- 0.4
	shoot mass	0.3	+/- 0.1	0.6	+/- 0.1	1.0	+/- 0.2

Mean total biomass was not affected by water depth (Table 1), but was reduced by clipping. Root mass decreased with clipping (1 g or less at all three water depths) and, when unclipped, decreased with water depth (5.2, 4.7, and 3.0 g, respectively; Tables 1 and 6).

Paspalidium punctatum

In the garden study, clipped plants had reduced survivorship in submersed treatments, starting in week 4, ($\hat{S}^*$ = 0.01-0.16; Table 2; Fig. 1), as did plants clipped every week in 0 cm water ($\hat{S}^*$ = 0.16). Unclipped plants grown in -13 cm water began to die after 14 weeks ($\hat{S}^*$ = 0.83), but, at other water depths, all unclipped plants survived ($\hat{S}^*$ = 1.00; Table 2; Fig. 1).

Total biomass was not directly affected by water depth (Table 1). Final root mass was higher in unclipped treatments at 0, -3, and -13 cm water (5.5, 6.4, and 3.2 g, respectively; Table 7) than unclipped treatments (0.5-1.6 g; Table 7). Most of the total biomass came from shoot mass in clipped plants (Table 7).

Table 6. Paspalum distichum. Means (X) and standard errors (S.E.) of total biomass (g), root mass (g), and shoot mass (g) at 3 water depths, 0 cm, -3 cm, and -13 cm, and 3 clipping levels, unclipped (C), biweekly (B; every two weeks) at soil level, and every week (W) all at soil level. Means for total biomass of clipped plants that differ significantly from controls by LSD analysis are indicated by a '*'. The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 to March 1986

		Water Depth (cm)					
		0		-3		-13	
		X	S.E.	X	S.E.	X	S.E.
	total biomass	9.5	+/- 1.0	8.5	+/- 0.9	9.8	+/- 0.7
C	root mass	5.2	+/- 2.1	4.7	+/- 0.9	3.0	+/- 0.6
	shoot mass	4.3	+/- 1.0	3.8	+/- 0.9	6.8	+/- 0.7
	total biomass	5.4	+/- 1.0*	5.9	+/- 0.8	4.2	+/- 0.7*
B	root mass	1.0	+/- 0.2	1.0	+/- 0.2	0.9	+/- 0.2
	shoot mass	4.5	+/- 1.0	4.8	+/- 0.8	3.4	+/- 0.7
	total biomass	3.0	+/- 0.3*	3.8	+/- 0.4*	4.6	+/- 1.0*
W	root mass	0.3	+/- 0.1	0.7	+/- 0.1	0.8	+/- 0.2
	shoot mass	2.7	+/- 0.3	3.1	+/- 0.4	3.8	+/- 1.0

Table 7. *Paspalidium punctatum*. Means (X) and standard errors (S.E.) of total biomass (g), root mass (g), and shoot mass (g) at 3 water depths, 0 cm, -3 cm, and -13 cm, and 3 clipping levels, unclipped (C), biweekly (B; every two weeks) at soil level, and every week (W) at soil level. Means for total biomass of clipped plants that differ significantly from controls by LSD analysis are indicated by a '*'. The garden study was conducted in a garden near the Keoladeo National Park, India, from November 1985 to March 1986

		Water Depth (cm)					
		0		-3		-13	
		X	S.E.	X	S.E.	X	S.E.
	total biomass	6.8	+/- 0.2	7.5	+/- 0.1	5.3	+/- 0.5
C	root mass	5.5	+/- 0.3	6.4	+/- 0.5	3.2	+/- 0.7
	shoot mass	1.3	+/- 0.2	1.1	+/- 0.1	2.1	+/- 0.5
	total biomass	3.3	+/- 0.3*	2.9	+/- 0.3*	1.2	+/- 0.2*
B	root mass	1.6	+/- 0.3	1.4	+/- 0.3	0.5	+/- 0.2
	shoot mass	1.7	+/- 0.3	1.5	+/- 0.3	0.7	+/- 0.2
	total biomass	2.6	+/- 0.3*	1.9	+/- 0.2*	2.0	+/- 0.2*
W	root mass	1.0	+/- 0.2	0.8	+/- 0.2	0.9	+/- 0.1
	shoot mass	1.6	+/- 0.3	1.2	+/- 0.2	1.1	+/- 0.2

DISCUSSION

Survivorship and Biomass Production

My initial hypothesis, that aquatic plants would eventually die when clipped underwater, was not always supported since only three of the four species died when clipped underwater. Nymphoides cristatum did not die when cut underwater. In contrast, none of the emergents died even when cut every two weeks in terrestrial conditions in the garden study (Table 2; Fig. 1). Nymphoides cristatum not only survived when clipped underwater, but died when grown in terrestrial conditions (Table 2; Fig. 1). What are the physiological and morphological bases for the variation in survival and growth at different water depths and clipping intensities among species?

The ability of an aquatic plant to mobilize root reserves to regrow shoots is critical if it is to survive clipping. The energetic costs of anaerobic respiration place a limit on the number of times below-ground reserves can be mobilized to regrow shoots (Sale and Wetzel 1983). If this is the reason for the differential response to clipping, then Nymphoides cristatum should have larger root reserves than the other three species, but the available evidence does not support this (Tables 4-7). Nymphoides cristatum's below-ground biomass is not greater than that of the other three species.

For a given species, an individual with a large root mass potentially can survive herbivory longer than one with a small root mass because it has more reserves. I examined whether individuals of a species with larger root masses survived longer than those with smaller root masses. Using regression analysis, survival was not correlated with root mass for any of these species (r^2 = 0.01-0.13; Fig. 2).

Morphological and developmental characteristics of these four species may also account for some of the differences observed in their survivorship. Ethylene production in *Nymphoides peltata* induces rapid stem elongation, which quickly puts submersed young leaves in contact with the air (Osborne 1982), and thus quickly reestablishes aerobic respiration. I observed that clipped shoots of *Nymphoides cristatum* were able to grow to the water surface in -13 cm of water in as little as 5 days, whereas the other species did not reach the water surface as quickly after clipping. As plant material protruding above the water column seems to be critical in the aeration of certain species (Hutchinson 1975; Dacey 1980; Dacey 1981; Etherington 1983; Raskin and Kende 1985; Howes et al. 1986) fast regrowth after clipping may be what distinguishes *Nymphoides* from the other three species.

Fig. 2. Number of weeks alive in the experiment vs. root mass for *Ipomoea aquatica* (r^2 =0.10, p=0.14), *Nymphoides cristatum* (r^2 =0.13, p=0.13), *Paspalum distichum* (r^2 = <0.01, p=0.97), and *Paspalidium punctatum* (r^2 = <0.01, p=0.92)

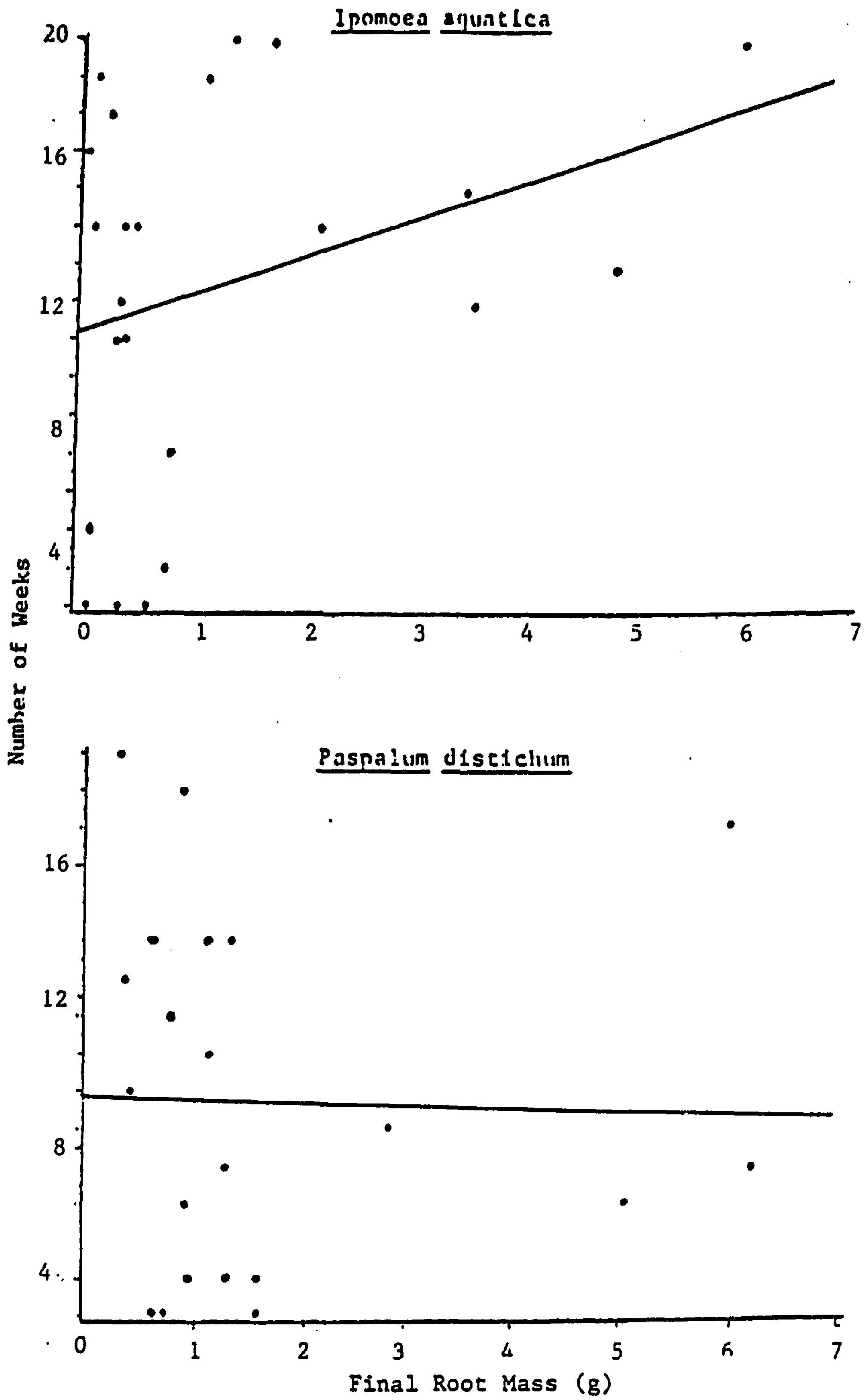
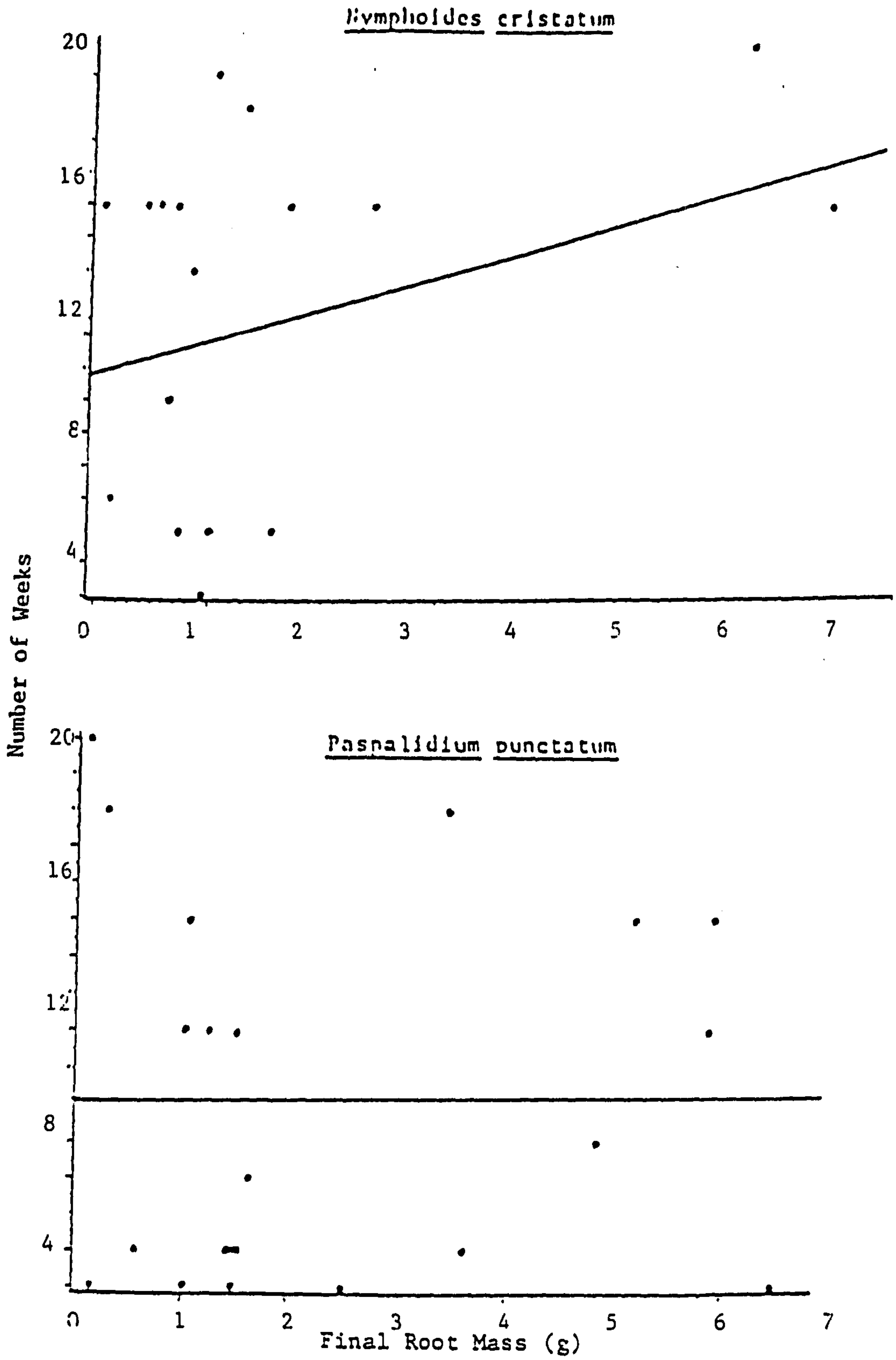

Ipomoea aquatica
20
16
12
8
4
0
1
2
3
4
5
6
7
Number of Weeks
Paspalum distichum
16
12
8
4
0
1
2
3
4
5
6
7
Final Root Mass (g)

Fig. 2. (Continued)


Nymphoides cristatum
Paspalidium punctatum
Number of Weeks
Final Root Mass (g)
20
16
12
8
4
0
1
2
3
4
5
6
7

Even though both field and garden emergent plants died when cut underwater, the responses were not identical. Field plants tended to die faster and after only one cutting (Table 3), while garden plants lived longer (Table 2; Fig. 1). Field plants may be more susceptible to dying after clipping than garden plants because of the conditions in the wetland, e.g., deeper water which can exceed 1 m and lower water clarity.

Differences in the survivorship among treatments suggest the use of estimates of continuous (Heisey and Fuller 1985) rather than apparent survivorship. If no plants die until the last interval of the experiment, then the values for continuous and apparent survivorship are the same. Otherwise, apparent survivorship overestimates and sometimes underestimates the actual length of survival for the treatment condition.

Although this experiment was designed to simulate grazing, the intensity of clipping by geese for a given plant in the field would vary. For Barheaded Geese grazing on mudflats in the Keoladeo National Park, field observations suggest that short cropping at soil level of new growth occurs almost immediately, and, in at least some cases, with a frequency exceeding once per week. For

Greylag Geese grazing underwater, while the frequency of grazing may be more than once per week, the stubble remaining after grazing varies in length and can be longer than in this study. Greylag Geese do not uproot plants in these wetlands as readily as they do in other locales. Stubble left underwater may escape further herbivory and regrow more rapidly than the repeatedly clipped plants.

Belsky (1986) concludes that the evidence for herbivory benefitting plants is sketchy since, among other problems, most studies supporting overcompensation rely only on the analysis of above-ground growth. For the four aquatic species in this experiment, undercompensation and exact compensation both occurred, but depended on water depth and clipping frequency for a given species.

Undercompensation, or when the total above- and below-ground biomass of a clipped plant is less than that of an unclipped plant, was the predominant response of plants which survived clipping in this experiment. Nymphoides cristatum however, exactly compensated when clipped every two weeks in either -3 or -13 cm of water (Table 5).

This study demonstrates that aquatic plants of Indian monsoonal wetlands have different inherent abilities to survive and grow after clipping; their tolerance depends greatly on the frequency of clipping and small differences in the water depth at which the plants are growing. Exact compensation could allow a species such as *Nymphoides cristatum* to benefit from grazing in aquatic situations where otherwise dominant macrophytes are being reduced by herbivory. This differential response of aquatic macrophytes has received little attention in the herbivory literature, but it is likely to be of great importance in structuring wetland vegetation subject to grazing. The results of my studies are consistent with the notion that goose grazing creates openings in the vegetation of monsoonal wetlands.

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SECTION 3. SUCCESSION AND GOOSE HERBIVORY IN MONSOONAL WETLANDS IN NORTHERN INDIA

Succession and Goose Herbivory in Monsoonal Wetlands In Northern India

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ABSTRACT

Seasonal changes in vegetation in monsoonal wetlands in the Keoladeo National Park, Bharatpur, India, are correlated with changes in mean water depth. Mean water depth was lowest just before the onset of the monsoon (June 1984; <1 cm), highest immediately after it (October 1985; 89 cm), and then declined slowly over the winter (March 1985; 14 cm) and spring. Mean cover of the dominant species, _Paspalum distichum_, was lowest just before the monsoon (June 1984; 19%), increased after the monsoon (October 1985; 35%), and reached its peak in late winter (March 1985; 49%). Long term drought, however, reduced the cover of _Paspalum distichum_ (March 1987; 2%). _Nymphaea nouchali_/_stellata_ was the next most abundant species after the monsoon (October 1985; 8% cover) but was not observed at other times of year (March 1984-March 1987; 0%). _Ipomoea aquatica_, _Panicum paludosum_, _Paspalidium punctatum_, and _Cyperus alopecuroides_, were uncommon, but occurred throughout the year (June 1984-March 1987; <1-2% cover).

The mean distance to open areas, i.e., areas free of emergent vegetation, along transects that would be grazed by geese was 193 m in October 1985, and, 43 m after grazing in March 1986. For transects that were not grazed by geese, no change in mean distance to open water patches was observed

(344 m and 339 m, in October 1985 and March 1986, respectively). Viable seeds were found in goose droppings, and these could be involved in re-vegetating openings.

Areas grazed by geese have a seed bank that contains 19-50 species per m^2 and 5,300 - 16,400 seeds per m^2 , as estimated by using a seedling assay technique. During the summer drawdown, annuals and seedlings of woody plants became established in areas grazed by geese, but no seedlings of any species were found in ungrazed areas. The seed bank contained many species that were not found as adult plants in either grazed or ungrazed sites. Field observations, however, indicated that clonal growth of surviving individuals was primarily responsible for the re-establishment of vegetation in open areas, and that recruitment from the seed bank is only of secondary importance.

INTRODUCTION

There are many parallels between the vegetation dynamics of wetlands of the prairie pothole region of North America and the monsoonal wetlands of India. Both undergo regular cyclic changes in water levels caused by rainfall patterns (wet-dry cycles) and associated changes in vegetation (Saxton 1924, Misra 1946, Gopal 1973, van der Valk 1981, Gopal 1986) and the vegetation of both is impacted by herbivores. There are also major differences.

Prairie wetlands have wet-dry cycles that occur over a period of 5 to 20 years or more (van der Valk 1981). In monsoonal wetlands, there are very pronounced seasonal changes in water levels as well as longer-term wet-dry cycles caused by periodic failure of the monsoon.

Grazing intensity in prairie wetlands is highly variable. It is mostly a function of the population size of a small mammal, the muskrat (*Ondatra zibethicus*), may be related to water depth (Kroeker 1988). In monsoonal wetlands, grazing intensity seems to be more constant and mostly the result of grazing by cattle, (*Bos taurus*) and water buffalo (*Bubalus bubalus* (Linnaeus)), as well as geese, coots, ducks, blue bull (*Boselaphus tragocamelus* Pallus), and sambhar (*Cervis unicolor* Kerr; Prater 1980) during the winter months, but very little is known about grazing intensities in these wetlands (Middleton and van der Valk 1987).

Seed banks play a major role in the vegetation dynamics of prairie wetlands. Seeds of several species types (submersed, floating-leaved, emergents, annuals) are present in their seed banks, and seeds of these species germinate under different water level conditions. As a result, the species composition of these wetlands can adjust quickly to changes in water level from year to year during a wet-dry cycle (van der Valk 1981). Nothing is known about the seed banks of monsoonal wetlands in India, but in Africa, seed banks enable annuals and emergents to become established on mudflats (Gaudet 1977).

This study examines the annual vegetation cycle in a monsoonal wetland over several years in north central India to determine how the vegetation changes in composition seasonally, whether there is a seed bank in these wetlands and what is its ecological significance. The impact of geese on the composition and structure of the vegetation was also investigated along with the role of geese as seed dispersal agents. If monsoonal wetlands have seed banks and their vegetation dynamics resulting from water level fluctuations are comparable to those in prairie wetlands, then the vegetation dynamics model of prairie wetlands developed by van der Valk (1981) would also be applicable to these wetlands.

METHODS

Study Site

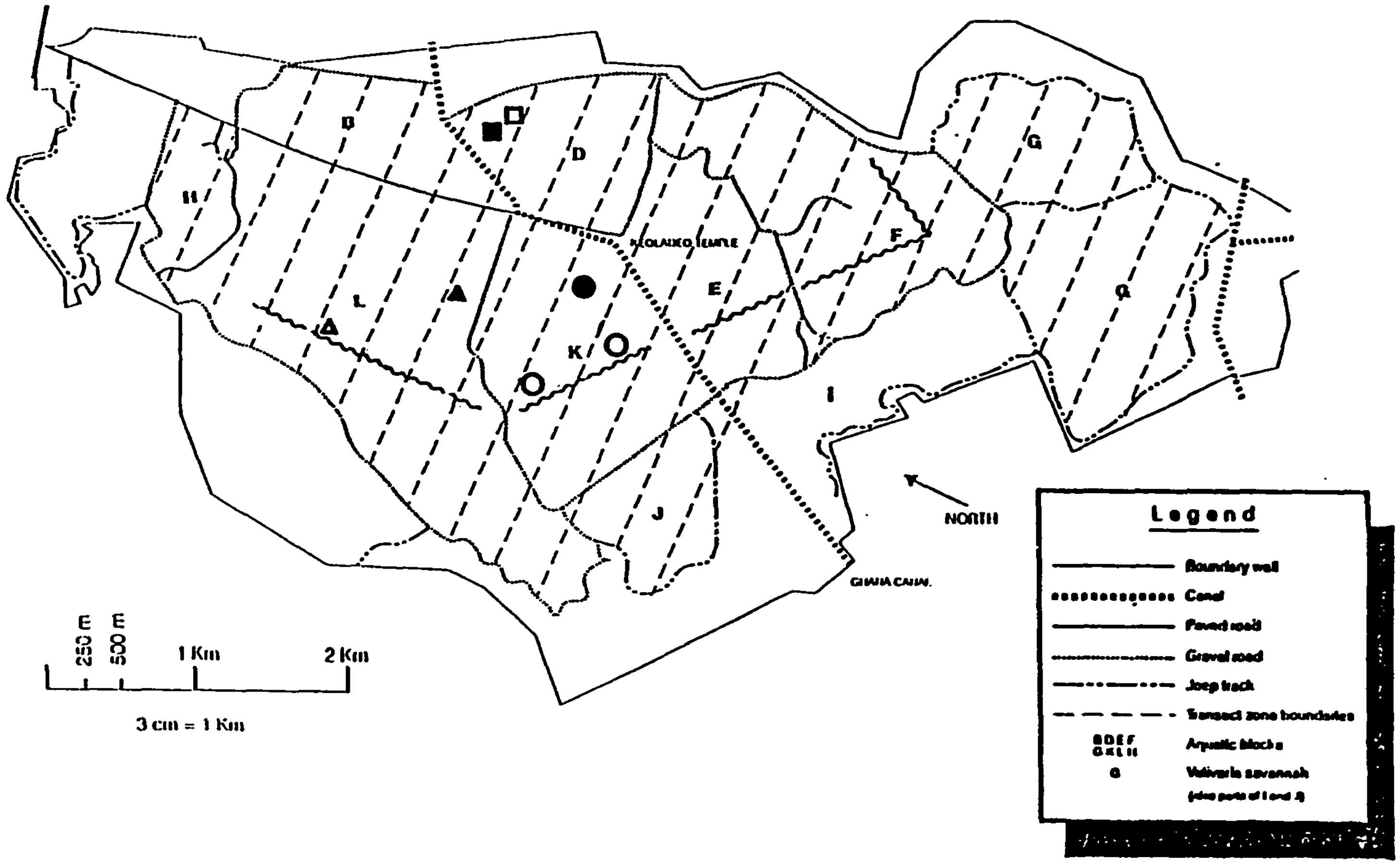
The Keoladeo National Park is a 29 km^2 mosaic of monsoonal wetlands, seasonally flooded savanna, and thorn woodland on the Indo-Gangetic Plain near Bharatpur, Rajasthan, India (27° 13'N Lat., 77° 32'E). The area is semiarid, receiving about 600 mm of rain each year. Water levels in the Park are controlled by floodgates and dams (Fig. 1; Ali and Vijayan 1986).

Prior to 1981, the area was used as a grazing commons for water buffalo and cows owned by local villagers. After the area's designation as a national park, domestic livestock grazing was banned (Ali and Vijayan 1986), but cutting of vegetation as fodder for livestock by villagers has continued.

Greylag (*Anser anser*) and Barheaded (*Anser indicus*) Geese annually overwinter in the Park from October to April. As many as 5,000 Greylag and 1,000 Barheaded Geese used the Park between November 1985 to April 1986. Greylag Geese graze in water up to 1.5 m deep, while Barheaded Geese mostly graze in shallower areas of less than 0.25 m, and even on drawndown wetlands outside of the Park used as grazing commons (personal observation). Flocks of these two species graze adjacent to one another, and at times,

Fig. 1. Map of the Keoladeo National Park, Bharatpur, India. Broken parallel lines indicate the location of transects used for the vegetation survey (March 1984 to March 1987). Recovery study sites are indicated by ■ , ▲ , and ● , in 'D', 'K', and 'L' blocks, respectively (January 1985 to April 1986). An open symbol indicates a grazed site; a closed symbol, an ungrazed site. The seed bank collection sites in goose grazed areas of L, K, E, and F Blocks are indicated by the undulating line (April 1986).

KEOLADEO NATIONAL PARK,BHARATPUR



isolated Barheads can be seen grazing with Greylags in deeper water. As water levels recede after the monsoon, both species of geese move into deeper sections of the wetland. Blue bull and sambhar both graze in aquatic areas, sambhar tending to graze in deeper areas than blue bull. Feral cows and pigs both follow the receding of the water into the wetland, though they generally graze at the edge of the water.

General Vegetation Surveys

General vegetation surveys of the aquatic blocks of the Park were carried out regularly, starting in March 1984 and ending in March 1987. The vegetation of the wetland blocks of the Park was sampled along 15 transects placed randomly within 330-m zones during each sampling period and traversing the wetland in an east-west direction (Fig. 1). One-m^2 quadrats were placed at 25 m intervals along these transects. The total number quadrats sampled in the surveys varied from 638-906. Quadrats affected by human disturbance were moved to the nearest undisturbed part of the wetland.

Cover of each plant species in a quadrat was estimated using the following scale: P = 1 plant with less than 1% cover, R = 2 plants of less than 1%, + = many small plants of less than 1%, 1 = 1-5%, 2 = 2-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75%, 6 = 76-95%, and 7 = 96-100%. Mean cover was calculated for each species by adding the midpoints of the cover classes for all occurrences in the survey and dividing by the total number of quadrats in the survey. Cover classes of less than 1% (P, R, and +) were assigned midpoints of 0.1, 0.2, and 0.3, respectively. During surveys beginning in October 1985, culm heights were measured in a 1/4-m^2 subsection of the quadrat by measuring the height of each culm.

Water depth was measured within each quadrat, and mean water depth was calculated for each aquatic block during a survey.

Open water, i.e., areas with less than 1% emergent or floating leaved plant cover were surveyed in October 1985 and March 1986, i.e., a period corresponding to before and after the most active periods of goose grazing in the Park. The distance to the nearest open water from each quadrat was measured by pacing. A transect was designated as "grazed" if goose droppings were found anywhere along the transect. A Wilcoxon 2-Sample Test was used to test to see if there was a difference in mean distances to open water from quadrats for grazed and ungrazed transects before and after the goose grazing season. Other grazers, especially ducks, were often found interspersed with geese along these grazed transects, but no grazers at all were detected along ungrazed transects.

Re-vegetation of Open Water Patches

From January 1985 to August 1986, the re-vegetation of areas cleared of emergent vegetation by geese were monitored at approximately 2 month intervals as were nearby ungrazed control areas. Within these grazed and ungrazed areas (Fig. 1), fifteen quadrats, 5 along each of 3 transects, were sampled in L, D, and K Blocks. At each site, 3 parallel transects were located at random within 25 m wide zones. In each quadrat, water depth was measured, and the cover of each species and bare ground was estimated.

Seed Bank Studies

General Seed Bank Study

During May 1984, seed bank samples were collected randomly at 10 sites in six different vegetation types dominated by *Eleocharis palustris*, *Ipomoea aquatica*, *Paspalum distichum*, *Hydrilla verticillata*, *Typha angustata*, and *Cynodon dactylon* (plant nomenclature is from Maheshwari, 1963). Vegetation types sampled occur in two hydrologically distinct areas:

a. aquatic areas that during normal monsoonal years have maximum water depths greater than 1.0 m and standing water for 9 months or more (*Eleocharis*, *Ipomoea*, *Hydrilla*, *Paspalum*, and *Typha*).

b. seasonally inundated areas that during normal monsoonal years have a maximum water depth between 10 cm and 50 cm and standing water for only 1 to 3 months (*Cynodon*).

At each sampling site, ten soil samples were collected to a depth of 5 cm, combined, and thoroughly mixed. This composite sample was sieved through a screen to remove rhizomes and was subsampled to fill 10 clay pots (30 cm diameter). There were 10 sites per vegetation type or 100 pots, and 600 pots altogether. Five pots from each sampling site were submersed under about 20 cm of water (flooded treatment) to simulate flooded conditions, and 5 others were kept moist by watering them daily (moist-soil treatment). The latter treatment was designed to simulate drawdown conditions (i.e., moist soil surfaces that were free of standing water). The treatment in which the highest seed germination for a species occurred was used to estimate its seed density.

All samples were kept in a seed bank shelter in the Park nursery. These shelters were enclosed with screening to prevent seeds from blowing into them and had a translucent fiberglass roof. Trees surrounding the area, however, shaded all the shelters to some extent during the day. As a result, both soil temperature maxima and light intensity were lower in the shelters than in the field, particularly in the moist-soil treatment.

Seed Bank of Goose Grazed Sites

In April 1986, a second seed bank study was initiated where the potential recruitment of seedlings was observed by gathering soil samples in goose grazed areas (Fig. 1). Forty samples in L, K, E, and F Block were collected randomly along a transect in areas of heaviest goose grazing (Fig. 1). Each sample consisted of the upper 5 cm of soil from a 1-m^2 area. Sample points were located randomly along each 50 m subsection of the transect.

Each sample was subsampled to fill ten 30 cm pots for a total of 400 pots. Five pots from each sample were placed under moist soil conditions and five were submersed as in the general seed bank study. All seedlings which emerged were recorded until March 1987.

Seed Dispersal by Geese

To determine if geese could play a role in seed dispersal, each month, from November 1985 to March 1986, Greylag and Barheaded Goose droppings were collected. One hundred droppings were collected and combined for each goose species each month (see Middleton and van der Valk (1987) for detailed methods).

Droppings were cleaned of debris, divided into four subsamples and placed into four 30 cm pots. Only droppings were placed in the pots and no soil underlay the droppings. Two pots were randomly assigned to a moist treatment and 2 pots to a submersed treatment with 13 cm of water above the surface of the droppings. The pots were placed in trays and covered with mosquito netting to keep out airborne seeds. Seedling emergence was observed until all droppings had decomposed in May 1986.

RESULTS

Seasonal Changes in Vegetation

Mean water depths in aquatic blocks were lowest, only <1 cm, just prior to the start of the rains in June 1984 (Table 1a). After an especially heavy monsoon, the mean water depth in aquatic parts of the Park rose to 89 cm in October 1985 (Table 1a). Water levels slowly declined over the winter, to 59 cm by March 1986 (Table 1b). The mean cover of _Paspalum distichum_ reached a peak in March (1984 and 1985; 51 and 41%, respectively; Table 1b), but was only 19% in June 1984, just prior to the monsoon (Table 1a). After the monsoon, as in October 1985, its mean cover was 35% (Table 1a), though its mean height (156 cm) was the highest at that time as it was for all species (Table 2).

There were some seasonal changes in the composition of the vegetation (Table 1a). During the fall high-water period after the monsoon (October 1985), water lilies, _Nymphaea nouchali/stellata_, had the second highest cover (8%), but they were not encountered in any of the other surveys (Tables 1a-b). Another floating leaved species, _Nymphoides cristatum_, was absent from the summer surveys (Table 1a). Annuals and woody seedlings were found only during drawdown, e.g., _Rumex dentatus_, an annual, and _Acacia_ seedlings (Table 1a).

Table 1a. Mean cover (%), species richness, and mean water depth (cm) of species with a frequency of more than 1% in at least one survey (excluding *Nymphoides indicum* and *Typha angustata*) found in the aquatic blocks of the Keoladeo National Park from June 1984 through October 1985

Species	June 1984	March 1985	Oct 1985
Algae	0	4	2
Acacia seedlings	<1	2	0
Cyperus alopecuroides	<1	<1	<1
Cyperus rotundus	<1	<1	<1
Cynodon dactylon	2	3	<1
Eichhornia crassipes	<1	<1	0
Hydrilla verticillata	<1	<1	<1
Ipomoea aquatica	<1	1	1
Nymphaea nouchali/stellata[a]	0	0	8
Nymphoides cristatum	0	<1	<1
Nymphoides indicum	0	0	0

[a] A designation such as *Nymphaea nouchali/stellata* indicates that there may have been more than one species in the genus present and that they were not distinguished in the survey.

Table 1a. (Continued)

Species	June 1984	March 1985	Oct 1985
Panicum paludosum	<1	<1	<1
Paspalidium punctatum	<1	<1	<1
Paspalum distichum	19	49	35
Rumex dentatus	<1	<1	0
Scirpus littoralis	<1	<1	<1
Scirpus tuberosus	<1	<1	<1
Sporobolus helvolus	1	2	<1
Typha angustata	<1	<1	0
OTHER	3	8	15
Total Cover	22	56	57
# of Quadrats	906	706	638
Species Richness	33	30	36
Mean Water Depth	<1	14	89

Table 1b. Mean cover (%) of species with more than 1% frequency in at least one survey, species richness, and mean water depth (cm) in the aquatic blocks of the Keoladeo National Park from March 1984 through March 1987

Species	March 1984	March 1986	March 1987
Algae	2	6	<1
Acacia seedlings	<1	0	<1
Cyperus alopecuroides	<1	<1	<1
Cyperus rotundus	0	<1	0
Cynodon dactylon	1	0	<1
Eichhornia crassipes	0	<1	<1
Hydrilla verticillata	2	<1	<1
Ipomoea aquatica	1	2	<1
Nymphaea nouchali/stellata	0	0	0
Nymphoides cristatum	<1	1	<1
Nymphoides indicum	0	<1	0

Table 1b. (Continued)

Species	March 1984	March 1986	March 1987
Panicum paludosum	<1	<1	<1
Paspalidium punctatum	0	<1	<1
Paspalum distichum	51	49	2
Rumex dentatus	<1	<1	<1
Scirpus littoralis	<1	<1	<1
Scirpus tuberosus	<1	<1	<1
Sporobolus helvolus	2	0	<1
Typha angustata	<1	<1	<1
OTHER	9	5	<1
Total Cover	61	62	3
# of Quadrats	755	708	768
Species Richness	31	32	33
Mean Water Depth	15	59	1

Table 2. Mean height (cm) of species of more than 47 cm in height during at least one survey in the aquatic blocks of the Keoladeo National Park from October 1985 through March 1987

Species	October 1985	March 1986	March 1987
Ipomoea aquatica	178	117	15
Nymphaea nouchali/stellata	47	0	0
Nymphoides cristatum	94	42	1
Panicum paludosum	119	94	5
Paspalidium punctatum	128	74	6
Paspalum distichum	156	107	14
Scirpus littoralis	138	98	8
Scirpus tuberosus	112	63	8

Species richness was higher after the monsoon (36 species; in October 1985; Table 1a) than at any other time of the year (30-33 species; Tables 1a-b).

Impact of an Extended Drought on the Vegetation

Because of the failure of the monsoon in 1986, a drought occurred in 1986 and 1987. Water levels receded during the fall of 1986 and winter to only 1 cm by March 1987 (Table 1b). By March 1987, the cover of Paspalum distichum was reduced to only 2% (Table 1b), and its mean height was only 14 cm (Table 2). The total cover of all species was reduced to only 3% (Table 1b).

Herbivory and Open Water Areas

Along transects in grazed areas, the distance to open water dropped from a mean of 193 m in October 1985 to 43 m in March 1986 (Table 3). For transects in ungrazed areas, there was no statistical difference between the October and March mean distances to open water (334 and 339 m, respectively; Table 3).

Table 3. Distance to openings (m) and Z values for ungrazed and grazed transects in the vegetation surveys in October 1985 and March 1986, before and after the most active period of goose grazing for Greylag and Barheaded Geese. Z values are based on a two-sided Wilcoxon 2-Sample Test

	Distance to Opening					
Transect Type	October 1985	March 1986	Quadrat Number	Z Value	p>Z	signif-icance
Ungrazed	334	339	80	0.27	0.78	n.s.
Grazed	193	43	512	18.11	0.00	s.

Vegetation Recovery In Goose Grazed Areas

In the recovery study, as would be expected, the total cover of ungrazed areas was much higher than grazed areas (Tables 4a-c). For example, in D Block in January 1985, the total cover in the ungrazed areas was 81% but in the grazed areas, it was only 19% (Table 4a). By April 1985, one month after goose grazing had ended in D Block, the total mean cover in this area was already 41% (Table 4a).

Perennials, i.e., *Paspalum distichum* had the highest mean cover in all grazed (8-55%; Tables 4a-c) and ungrazed areas (57-98%; Tables 4a-c). Although annuals and woody seedlings were not found in ungrazed areas, they were found in grazed areas, especially during the summer drawdown (Tables 4a-c; see APPENDICES IIa-c for species listed by mean cover in each area; Middleton 1989). Grazed areas had higher species richness after grazing (4-11 total species) than ungrazed areas (2-4 total species; Tables 4a-c) when free-floating species are excluded. These species were eliminated from the consideration since they are temporary occupants of specific quadrats, moving freely with water currents.

Table 4a. Mean cover (%) and life history category of species for an ungrazed site and a site grazed by Barheaded Geese in D Block (15 quadrats at each site)

Life History Category	Ungrazed 1/85	Ungrazed 4/85	Ungrazed 6/85	Grazed 1/85	Grazed 4/85	Grazed 6/85
annual	0.0	0.0	0.0	0.0	0.0	0.0
bulbous sprouter	0.0	0.9	0.0	0.0	0.0	0.0
winter seasonal	0.0	0.5	0.0	0.0	0.0	0.0
perennial	82.4	97.6	97.5	19.1	40.6	53.7
woody seedlings	0.0	0.0	0.0	0.0	0.0	0.0
floaters	1.5	0.0	0.1	26.6	0.0	0.0
Total	82.1	97.6	97.5	45.7	40.6	53.7
w/o floaters	81.2	97.6	97.5	19.1	40.6	53.7
Species Richness	7	3	2	5	6	5
w/o floaters	4	3	2	4	5	4

Table 4b. Mean cover (%) and life history category of species for an ungrazed site and a site grazed by Barheaded Geese in L Block (15 quadrats at each site)

Life History Category	Ungrazed			Grazed		
	3/86	6/86	8/86	3/86	6/86	8/86
annual	0.0	0.0	0.0	<0.1	0.0	<0.1
bulbous sprouter	0.0	0.0	0.0	1.3	0.7	0.6
winter seasonal	5.7	0.0	0.0	0.0	0.0	0.0
perennial	77.9	95.4	59.3	8.2	22.2	27.2
woody seedlings	0.0	0.0	0.0	0.0	0.0	0.2
floaters	4.6	0.0	0.4	0.0	0.0	0.0
Total	88.0	95.4	59.7	9.5	22.9	28.0
w/o floaters	83.4	95.4	59.3	9.5	22.9	28.0
Species Richness	7	4	4	8	10	11
w/o floaters	3	3	3	8	10	11

Table 4c. Mean cover (%) and life history category of species for an ungrazed site and 2 sites grazed by both Barheaded and Greylag Geese in K Block (15 quadrats at each site)

Life History Category	Ungrazed			Grazed #1			Grazed #2		
	3/86	5/86	6/86	3/86	5/86	6/86	3/86	5/86	6/86
annual	0.0	0.0	0.0	<0.1	<0.1	4.4	0.0	0.9	3.0
bulbous sprouter	0.0	0.0	0.0	3.3	8.6	1.7	0.0	0.7	1.0
winter seasonal	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
perennial	59.4	82.6	57.2	46.8	90.7	28.0	19.9	55.3	24.7
woody seedlings	0.0	0.0	0.0	0.0	0.0	0.2	0.0	<0.1	0.0
floaters	25.7	3.3	3.0	3.2	0.0	<0.1	<0.1	<0.1	0.0
Total	90.6	85.9	60.2	53.3	99.3	34.4	19.9	56.9	30.3
w/o floaters	64.9	82.6	57.2	50.1	93.3	34.4	19.9	56.9	30.3
Species Richness	6	3	3	9	6	10	5	7	10
w/o floaters	3	2	2	7	6	10	4	6	10

The Seed Bank

General Survey

In the 1984 seed bank survey, species richness was found to be highest in the Cynodon dactylon sites (48 species; Table 5). The Typha angustata had the lowest number of species (19 species; Table 5).

The upper 5 cm of soil had a total seed density of 5,300 - 16,400 seeds/m^2 (Table 6). Paspalum distichum was widespread in the seed banks of vegetation types dominated by the emergents Paspalum distichum, Ipomoea aquatica, and Eleocharis palustris (83, 5, and 25 seeds/m^2 , respectively; Table 6); and by the submersed species, Hydrilla verticillata (1 seed/m^2 ; Table 6); and by Typha angustata (6 seeds/m^2 ; Table 6) but no seeds were found of this species in shallow areas dominated by Cynodon dactylon (Table 6).

Perennial species were found in all vegetation types including Nymphoides cristatum/indicum (1-61 seeds/m^2), Najas graminea/minor (49-1200 seeds/m^2), Sporobolus helvolus/Cynodon dactylon (4-445 seeds/m^2), and Vallisneria spiralis (4-463 seeds/m^2). Other perennials which were absent in one vegetation type included Nymphaea nouchali/stellata (1-10 seeds/m^2), Ammania auriculata (0-120 seeds/m^2), and Cyperus difformis (0-520 seeds/m^2 ;

Table 5. Total number of species in the seed bank of the aquatic vegetation types (collected May 1984), potential vegetation (seed bank) of goose grazed areas (collected April 1986), field sites either grazed or ungrazed by geese (30 quadrats each, tallied in from January 1985 to August 1985) and goose droppings (collected November 1985 to April 1986) in the Keoladeo National Park

Vegetation Type	Block(s)	Major Species	Minor Species	Total Species
Eleocharis palustris	E	11	24	35
Ipomoea aquatica	E	6	19	25
Paspalum distichum	E	5	26	31
Hydrilla verticillata	E	8	17	25
Typha angustata	N	9	10	19
Cynodon dactylon	B	24	24	48
Potential Goose Grazed	L,K,E,F	4	40	44
Grazed Field Sites	L,K	2	11	13
Ungrazed Field Sites	L,K	0	0	0
Goose Droppings	ALL	3	0	3

Table 6. Mean number of seeds per m^2 in the vegetation types: *Paspalum distichum* (Pas), *Ipomoea aquatica* (Ipo), *Eleocharis palustris* (Ele), *Hydrilla verticillata* (Hyd), *Cynodon dactylon* (Cyn), and *Typha angustata* (Typ) in the Keoladeo National Park

Species	Pas	Ipo	Ele	Hyd	Cyn	Typ
Acacia nilotica	<1	<1	<1	0	<1	0
Alternanthera sessilis	0	0	0	0	3	0
Ammania auriculata	0	2	11	1	120	1
Bergia ammannioides	0	0	<1	0	21	0
Blumea bifoliata	0	0	<1	<1	14	0
Brassica campestris	0	0	<1	0	0	0
Cassia tora	<1	0	0	0	0	0
Chara sp. (spores)	354	146	293	253	60	67
Commelina forskalii	0	0	0	0	<1	0
Cyperus alopecuroides	7	3	24	1	0	0
Cyperus difformis	<1	<1	<1	<1	520	0
Cyperus iria	0	0	1	0	44	0
Cyperus rotundus	0	0	0	0	18	0
Cyperus triceps	<1	0	0	0	0	0
Dactyloctenium aegyptium	0	0	0	0	22	0

Table 6. (Continued)

Species	Pas	Ipo	Ele	Hyd	Cyn	Typ
Echinochloa crusgalli	0	0	<1	0	188	0
Eichhornia crassipes	0	0	2	<1	0	0
Elatine triandra	5	0	72	7	553	0
Eleocharis atropurpurea	2	0	11	1	333	0
Eleocharis palustris	0	0	1	<1	0	<1
Eragrostis sp.	0	0	0	0	<1	0
Erigeron bonariensis	<1	<1	0	<1	0	0
Euphorbia orbiculata	0	0	0	1	0	0
Glinus lotoides	0	0	0	0	1	0
Glinus oppositifolia	1	3	9	0	289	0
Gnaphalium polycaulon	1	0	0	<1	16	0
Gnaphalium pulvinatum	0	0	0	0	1	0
Grangea maderaspatana	1	2	4	2	13	0
Hemiadelphus polyspermus	0	<1	<1	0	118	0
Hydrilla verticillata	15	169	133	448	0	13
Hydrolea zeylandica	<1	0	0	0	3	0
Ipomoea aquatica	2	2	3	0	0	0
Limnophila indica	<1	0	2	0	34	0
Lindernia parviflora	0	0	0	0	21	0

Table 6. (Continued)

Species	Pas	Ipo	Ele	Hyd	Cyn	Typ
Linum usitatissimum	0	0	0	0	1	0
Ludwigia perennis	<1	0	0	0	47	1
Marsilea minutea	0	0	0	0	2	0
Najas graminea/minor	102	1200	464	1769	49	504
Nymphaea nouchali/stellata	1	1	6	3	10	0
Nymphoides cristatum/indicum	4	16	34	17	1	11
Panicum paludosum	0	0	0	0	<1	0
Paspalidium punctatum	<1	2	7	0	0	0
Paspalum distichum	83	5	25	1	0	6
Polygonum plebeium	0	0	0	0	5	1
Polypogon monspeliensis	0	1	0	1	0	0
Potamogeton crispus	0	2	0	0	0	0
Potamogeton nodosus	1	<1	<1	50	0	0
Potentilla supina	<1	0	<1	0	2	1
Prosopis juliflora	2	0	<1	0	0	1
Pulicaria crispus	0	0	0	0	3	0
Rotala densiflora	1	0	1	0	50	0
Rumex dentatus	0	1	1	1	<1	0
Sagittaria guayanensis	1	2	6	3	37	0
Salvadora persica	0	0	0	0	1	0

Table 6. (Continued)

Species	Pas	Ipo	Ele	Hyd	Cyn	Typ
Scirpus articulatus	0	1	0	0	297	0
Scirpus supinus/roylei	0	0	8	13	357	0
Scirpus tuberosus	<1	0	<1	0	<1	<1
Sphenoclea zeylandica	0	0	0	0	2	0
Sporobolus helvolus/Cynodon	445	199	257	61	4	39
Tamarix aphylla	0	<1	0	0	0	0
Tenagocharis latifolia	0	0	0	0	<1	0
Trianthema portulacastrum	0	0	0	0	5	0
Typha angustata	4	<1	3	0	1	673
Vallisneria spiralis	7	74	212	463	4	207
Vetiveria zizanioides	0	0	0	<1	0	0
unknown dicot #1	0	0	0	0	5	0
unknown dicot #2	20	0	0	0	10	0
Total	1059	1831	1590	3096	3283	1525

Table 6). Certain other perennials were found sporadically in the seed banks of these vegetation types including Bergia ammannioides (0-21 seeds/m^2), Glinus oppositifolia (0-289 seeds/m^2), Hydrolea zeylandica (0-3 seeds/m^2), Ludwigia perrenis (0-47 seeds/m^2), and Hydrilla verticillata (0-448 seeds/m^2 ; Table 6).

Annual species such as Polygonum plebeium, Rumex dentatus, Cyperus difformis, Echinochloa crusgalli, and Dactyloctenium aegyptium, were found in the seed banks, but none of these species were found in all vegetation types (0-520 seeds/m^2 ; Table 6).

Similarly, woody plants such as Acacia nilotica, Prosopus juliflora, and Salvadora persica were found in some vegetation types, but all were absent in the Hydrilla verticillata vegetation type (0-4 seeds/m^2 ; Table 6).

Seed Bank of Goose Grazed Sites

The seed bank of these goose grazed areas, had a total of 5,200 seeds/m^2 of 44 species in the upper 5 cm of soil (Table 7). Perennial plants were the most commonly observed life history category to germinate from the seed bank of the goose grazed sites (858 seeds/m^2 ; Table 7), with a large number of seeds from Paspalum distichum, Hemiadelphus polyspermus, Nymphaea nouchali/stellata, Bergia

Table 7. Potential vegetation of goose grazed areas estimated for the seed bank study (seeds/m^2) and the actual vegetation (seedlings/m^2) of grazed sites observed from January 1985 to August 1985 in L and K Blocks (30 quadrats). Life history categories (LHC) are as follows: A=annual, B=bulbous resprouter, F=floater, P=perennial, S=Winter Seasonal, and W=woody

Species	LHC	Potential	Actual
Acacia nilotica	W	0	<1
Aeschynomene indicum	A	<1	0
Ageratum conyzoides	A	<1	0
Alternanthera sessilis	P	<1	0
Ammania auriculata	P	1	<1
Bergia ammannioides	P	95	0
Caesulia axillaris	P	<1	0
Cassiotropa sp.	W	0	<1
Ceratophyllum demersum	F	2	0
Coronupis didymus	P	<1	0
Cyperus alopecuroides	P	<1	0
Cyperus difformis	A	<1	0
Cyperus rotundus	B	4	0
Echinochloa crusgalli	A	13	<1

Table 7. (Continued)

Species	LHC	Potential	Actual
Eichhornia crassipes	P	<1	0
Ficus benghelensis	W	3	0
Gnaphalium polycaulon	S	8	<1
Hemiadelphus polyspermus	P	277	0
Hydrilla verticillata	P	<1	0
Kirgonelia reticulata	W	0	<1
Laggera aurita	P	3	0
Lantana indica	W	<1	0
Limnophila indica	S	16	0
Melochia corchorifolia	W	2	0
Mitragyna parviflora	W	29	0
Najas graminea/minor	P	41	0
Nothosaerva brachiata	P	<1	0
Nymphaea nouchali/stellata	S	99	0
Nymphoides cristatum/indicum	P	6	0
Oryza rufipogon	A	<1	<1
Panicum paludosum	P	<1	0
Paspalum distichum	P	428	0
Polygonum plebeium	A	<1	<1
Polypogon monspelienis	A	<1	0

Table 7. (Continued)

Species	LHC	Potential	Actual
Potamogeton crispus	P	<1	0
Potamogeton nodosus	P	<1	0
Potentilla supina	S	2	<1
Prosopis julifora	W	<1	<1
Rumex dentatus	A	<1	<1
Sagittaria guayanensis	S	<1	0
Scirpus littoralis	P	<1	0
Scirpus supinus/roylei	P	2	0
Setaria sp.	A	0	<1
Spirodela polyrhiza	F	<1	0
Sporobolus helvolus/Cynodon	A/P	<1	0
Syzgium cumini	W	<1	0
Typha angustata	P	<1	0
Vallisneria spiralis	P	5	0
unknown dicot #1	-	0	<1
Total		1036	<1

ammannioides, and Najas graminea (428, 277, 99, 95, and 41 seeds/m^2, respectively; Table 7).

Winter seasonal species were the second most commonly observed life history category (125 seeds/m^2; Table 7) and included species such as Limnophila indica, Gnaphalium polycaulon, and Nymphoides cristatum/indicum (Table 7).

Woody species included Mitragyna parviflora, Ficus benghelensis, Melochia corchorifolia, Prosopus juliflora, Lantana indica, and Syzgium cumini (29, 3, 2, <1, <1, and <1 seeds/m^2, respectively; Table 7).

Annuals included species such as Echinochloa crusgalli (13 seeds/m^2) and Aeschynomene indica, Cyperus difformis, Oryza rufipogon, Polygonum plebeium, Polypogon monspeliensis, and Rumex dentatus (<1 seed/m^2; Table 7).

No seedlings emerged in ungrazed areas of the wetland, though in grazed wetland sites, < 1.0 seedlings/m^2 of 13 species were observed (Table 8).

Seeds in Goose Droppings

A total of 687 seeds/m^2 of 3 species germinated from goose droppings (Table 8). Seeds germinated from goose droppings collected in November 1985 samples and not from those collected any other month. In the moist-soil

Table 8. Mean number of seeds per m^2 in Greylag Goose droppings subjected to moist-soil (MS) and flooded (FL) treatments. The droppings were collected on November 20, 1985 (2 pots per treatment). No seeds germinated from Greylag droppings collected between December 1985 and April 1986 or from Barheaded Goose droppings collected in any month. Life history categories (LHC) are as follows: A=annual, B=bulbous resprouter, S=Winter Seasonal, P=perennial, W=woody

Species	LHC	MS	FL
Paspalum distichum	P	616 +/- 62	-
Scirpus tuberosus	B	64 +/- 30	-
Potamogeton indicus	P	-	7 +/- 10
Total		680	7
Species Richness		2	1

(dropping) treatment, two species were found, Paspalum distichum (616 seeds/m^2 of droppings), and Scirpus tuberosus (64 seeds/m^2 of droppings). In the submersed treatment, seeds of Potamogeton indicus were observed (7 seeds/m^2 ; Table 8).

DISCUSSION

Seasonal Changes In Vegetation

Previous studies of monsoonal wetlands in northern India have shown that they change greatly in species composition throughout the year. During the annual drought, the vegetation of the mudflats typically is comprised of annuals (Saxton 1924, Misra 1946, Gopal 1986), e.g., *Polygonum plebeium* and scattered trees and shrubs (some very small and presumably seedlings) of *Acacia*, *Capparis*, *Ziziphus*, and *Prosopus* (Saxton 1924). During the monsoon, emergent plants such as *Andropogon annulatus*, and *Ipomoea aquatica* are the dominants in areas with standing water (Saxton 1924).

In contrast, the composition of the vegetation of North American prairie wetlands does not change greatly seasonally. Neither does that of the wetlands of the Keoladeo National Park because of the overwhelming dominance of *Paspalum distichum*. Prior to 1981, *Paspalum distichum* was inconsequential in the Park and the composition of the vegetation was dominated by annuals, emergents, submersed, and floating-leaved species just as in other grazed wetlands of the region (van der Valk, personal observation, Department of Botany, Iowa State University, Ames, Iowa). Now, the major seasonal change that occurs is in the cover of *Paspalum distichum* (Table 1a-b), although some minor seasonal changes in composition continue to occur. Even in areas heavily grazed by geese where as much as 80% of the ground is bare, their rapid revegetation is primarily as a result of the clonal growth of Paspalum distichum and very few seedlings are recruited from the seed bank (<1 seedling/m^2 ; Table 5).

Despite the proliferation of Paspalum distichum, at least 48 species were present, most as minor components of the vegetation (Table 5). There are no estimates of the number of species that were present prior to the cessation of water buffalo grazing. The seed bank, however, contained 67 species (Table 7), and this suggests that species that formerly were present in the vegetation are no longer present. This is consistent with other studies which link grazing to higher species diversity (Harper 1977, McNaughton 1983) and, the cessation of grazing to a drop in species diversity (Tansley and Adamson 1925, Edroma 1981). In a North American prairie wetland, Eagle Lake, Iowa, 50 species were observed in a vegetation survey (van der Valk and Davis 1978).

Wet/Dry Cycles in Wetlands

Following the failure of the monsoon in the summer of 1986, a combination of very low water levels and grass cutting resulted in the mean total cover of plants being reduced to only 3% by March 1987 (Table 1b). With such a small amount of plants cover, the seed bank could become more important in the re-establishment of species. Periodic droughts are a regular feature of the climate of northern India. These droughts influence monsoonal wetland vegetation in major ways. Unfortunately, we have no data about plant recruitment and revegetation after the drought, but on the basis of anecdotal information available to us, there has been a significant decrease in Paspalum distichum, and, after the wetland reflooded, an increase in the abundance of floating-leaved and submersed species.

The Formation of Openings in Wetlands

The role of muskrats in creating open water areas is well documented in the prairie wetlands of North America (Weller and Spatcher 1965). In northern India, herbivores such as domestic water buffalo are able to eliminate all emergents in a monsoonal wetland in a matter of months following the monsoon (personal observation). The Keoladeo National Park is atypical of northern Indian wetlands, since water buffalo grazing has been banned since 1981 (Ali and Vijayan 1986). Geese seem to create openings in dense stands of Paspalum distichum. Much of the aquatic area of the Park was grazed by geese, but only small open areas were produced. By March 1987, after the prolonged drought, 99% of the aquatic areas had been grazed by feral cows and pigs (Davis et al. 1989).

The maintenance of openings by aquatic herbivores is due largely to the inability of many species to grow well after being cut underwater (Middleton 1989). Field studies corroborate these results. In North America, simulated muskrat grazing studies showed lower regenerative potential and growth after cutting underwater in *Scirpus olneyi* (McCabe and Wolfe 1988). In India, simulated goose grazing experiments showed that three species of emergent plants (*Paspalum distichum*, *Ipomoea aquatica*, and *Paspalidium aquatica*) died when cut underwater, but not when clipped in terrestrial conditions. Not all species die when clipped underwater. For example, one floating-leaved species, *Nymphoides cristatum*, lived when cut underwater (Middleton 1989). In field clipping studies in the Keoladeo National Park, *Paspalum distichum* and *Ipomoea aquatica* also died when cut underwater (Middleton 1989).

In addition to reducing the standing biomass of certain species (Tables 4a-c), herbivores may introduce seeds into grazed areas. Dispersal of seeds by herbivores is better studied in terrestrial situations (Janzen 1981; Lieberman and Lieberman 1987). In aquatic situations, improved seed germination has been linked to ingestion of seeds by ducks and fish (Agami and Waisel 1986; Agami and Waisel 1988).

Geese, in the Keoladeo National Park, eat at least 8 species of seeds (Middleton and van der Valk 1987), of which 3 species germinated from goose droppings (Table 8). None of these species, however, were observed as seedlings on grazed sites, (Table 7), but the potential exists for geese and other herbivores to alter re-establishment patterns of plants in monsoonal wetlands.

Seed Banks In Wetlands

During drawdown, seed banks in prairie wetlands of North America enable the re-establishment of emergent and annual species and, when there is standing water, the establishment of submersed and free-floating species (van der Valk and Davis 1978). Depending on water level conditions and muskrat populations, these species replace each other in a series of cyclical vegetation changes (van der Valk 1985).

During our study, the seed bank of the Keoladeo National Park seemed to be much less important than those of prairie wetlands. Seed density is higher in the seed banks of prairie wetlands. Eagle Lake, Iowa had 21,445 to 42,615 seeds per m^2 (van der Valk and Davis 1978) while the monsoonal wetland of the Keoladeo National Park had only 5,300 - 16,400 seeds per m^2 (Table 8). Eagle Lake had only 8 and 13 species per m^2 in submersed and drawdown conditions, respectively (Table 8). In the Keoladeo

National Park, there were a mean of 16 and 24 species per m^2 in submersed and drawdown conditions, respectively (Table 8). The cover of Paspalum distichum plants and litter limits the germination of seeds (Davis et al. 1988).

Grazing removes dominant vegetation and may allow an opportunity for invasion, i.e., an invasion window (Johnstone 1986). In the Keoladeo National Park, openings created by geese and other aquatic herbivores were invaded by 13 species during the summer drawdown, some of them annuals and woody species (Table 5). No seedlings of any species were found on ungrazed sites (Table 5). Many more species were found in the seed bank of these grazed sites than were found in the field during summer drawdown. A careful analysis of the germination dynamics of these species would no doubt delineate the seasonal aspect of germination in these monsoonal wetlands.

The role of the seed bank in the annual cycle of the wetland in the Keoladeo National Park has been significantly reduced by the growth of Paspalum distichum. The re-establishment of annual and emergent species from the seed bank as occurs in North American prairie wetlands probably also occurs in northern India where they are grazed by water buffalo.

The seed bank of the Park is quite diverse and to some extent must reflect the composition of its vegetation before the proliferation of Paspalum distichum. Many species common in the seed bank were never encountered in the field including Bergia ammannioides, Hydrolea zeylandica, Ludwigia perrenis, Limnophyllum indicum, and Ammania auriculata (Table 6). These genera were reported as being common in the vegetation developing toward the end of the monsoon season in the north Indian wetland studied by Saxton (1924).

On Lake Naivasha, Kenya, vegetation on mudflats is re-established by perennating structures and seeds. There, the dominant species, Cyperus papyrus, commonly starts from seed on mudflats and competes for a time with an annual species of Polygonum. The formation of bands of vegetation in these African wetlands seems to be related to grazing by cattle and hippos (Gaudet 1977) and, in fact, heavy grazing by domestic animals or cutting of monsoonal wetlands for fodder or building material (Maltby 1986; Nair 1986; Al-Saadi and Al-Mousawi 1988) is common worldwide.

In conclusion, the cyclic succession model developed for temperate prairie wetlands of North America (van der Valk 1981), appropriately modified to take into consideration the life-history characteristics of monsoonal wetland species, could be used to predict seasonal and longer term changes in the composition of the vegetation of monsoonal wetlands caused by water level changes. However, it is not applicable to the wetlands of the Koeladeo National Park because grazing intensities are no longer sufficient to remove the emergent vegetation and allow recruitment from the seed bank.

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GENERAL SUMMARY

The goal of this project was to compare the role of herbivory in the succession of monsoonal wetlands in the Keoladeo National Park, India, with that of prairie glacial marshes of North America.

Emergent species in both situations die after being cut underwater. In Michigan, when *Typha* was clipped underwater, anaerobic respiration and death eventually resulted (Sale and Wetzel 1983). In a garden experiment in this study, three emergent species died when clipped underwater, *Paspalum distichum*, *Ipomoea aquatica*, and *Paspalidium punctatum*. When clipped underwater, another species, *Nymphoides cristatum*, lived and grew as much as unclipped plants (exact compensation; Belsky 1986). In a field study, *Paspalum distichum*, and *Ipomoea aquatica*, the only species tested, both died when clipped underwater. This differential response of species to clipping underwater could be important in the vegetation dynamics of wetlands experiencing herbivory.

Selection of species for experiments was based on a food habits study of Greylag and Barheaded Geese. *Paspalum distichum* constituted 45-68% of the annual diet of these geese, and comprised 2-51% of the cover of plants in the Park. The other three species were all eaten by geese (<1-2% of the annual diet) and were common during most seasons (0-2% cover).

Muskrat herbivory and high water in prairie glacial marshes produce an open lake (Weller and Spatcher 1965) which does not re-vegetate with emergents until drought which occurs at 5-25 year intervals (van der Valk 1981). High water levels are present only after the rainy season (October to March) in monsoonal wetlands, and annual drawdown occurs in the summer (April to June). Drought can be extended by the failure of the monsoon.

While much of the Park was grazed by geese in October 1985 to March 1986, only heavily grazed areas actually became open water or mudflat. The aerial extent of openings increased on goose grazed sites and not on ungrazed sites in the Keoladeo National Park although, geese and other herbivores were not able to remove all emergent and floating-leaved species in the monsoonal wetlands of the Park. Apparently, muskrats and high water in prairie glacial marshes of North America are more efficient than herbivores in the Keoladeo National Park in eliminating vegetation.

Re-vegetation of these openings occurred during drawdown by clonal spreading of surviving plants, and not by recruitment from the seed bank, as in prairie glacial marshes (van der Valk and Davis 1978). In the Keoladeo National Park, seeds of annuals and woody species germinated on goose grazed sites but not on ungrazed sites, suggesting that grazing can provide an invasion window for these life history types.

After the cessation of water buffalo grazing in 1981, Paspalum distichum began to dominate the vegetation in the Park (Ali and Vijayan 1986), persisting even into the summer. Outside of the Keoladeo National Park, mudflat conditions prevail during the drought and a variety of annuals invade, including Polygonum plebeium (Saxton 1924, Gopal 1986), similar to the more localized invasion of annuals on goose grazed sites in this study. Before 1981, it is likely that the seed bank played a larger role in the establishment of vegetation during drawdown. Because of the spread of Paspalum distichum in the Keoladeo National Park, the seed bank no longer seems to play a significant role in the wetlands of the Park.

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APPENDIX: VOUCHER PLANT LIST FOR SPECIMENS COLLECTED IN THE KEOLADEO NATIONAL PARK, BHARATPUR, INDIA. (All specimens are stored in the Ada Hayden Herbarium of Iowa State University, Ames, Iowa)

Species	Middleton #
Acacia nilotica (L.) Del. subsp. indica (Benth.) Brennan.	1047
Acacia nilotica (L.) Del. subsp. indica (Benth.) Brennan.	1077
Acacia senegal Willd.	1032
Achyranthes aspera Hook.	1013
Aeschynome indica Linn.	1011
Allopteris cimicina (L.) Stapf.	1008
Alternanthera sessilus (Br.) D.C.	1046
Amaranthus tenuifolius Willd.	1089
Amaranthus viridus L.	1048
Amischophacelus axillaris (L.) Rolla.	1091
Ammania auriculata Willd.	1033
Azadirachta indica A. Juss.	1028
Azolla pinnata R. Br.	1050
Balanites aegyptica	1045
Bergia ammannioides Roxb.	1097

Blumea obliqua (Linn.) Druce.	1104
Bracharia reptans (L.) Gardn. & Hubb.	1007
Capparis sepiaria L.	1099
Cassia tora L.	1035
Cassia tora L.	1100
Cenchrus ciliaris L.	1009
Ceratophyllum demersum L.	1053
Chenopodium album L.	1086
Chloris virgata Sw.	1094
Cochlearia cochlearioides (Roth.) Santapau & Mahesh.	1105
Commelina benghalensis Linn.	1092
Commelina forskalaei Vahl.	1044
Commelina forskalaei Vahl.	1087
Conyza bonariensis (L.) Cronquist	1090
Corallocarpus epigaeus (Rottb. et. Willd.) Clarke.	1098
Cotula hemisphaerica (Roxb.) Wall ex. Benth.	1103
Cynodon dactylon Pers.	1057
Cynodon dactylon Pers.	1069
Cyperus alopecurioides Rottb.	1076
Cyperus difformis L.	1020
Cyperus rotundus L.	1073
Dactyloctenium aegyptium (L.) Willd.	1093
Datura fastuosa L.	1038

Digitaria ciliaris (Retz.) Koel.	1022
Echinochloa colonum (L.) Link.	1018
Eleocharis palustris R. Br.	1066
Elytraria acaulis (L.F.) Lindau.	1001
Eragrostis ciliaris R. Br.	1021
Eriochloa procera (Retz.) C.E. Hubb.	1005
Eruca sativa Mill.	1054
Gnaphalium indicum Linn.	1101
Gnaphalium polycaulon Pers.	1102
Hemiadelphus polyspermus (Roxb.) Nees.	1068
Ipomoea aquatica Forsk.	1070
Iseilema laxum Hack.	1016
Kirgonelia reticulata (Poir.) Baill.	1049
Lepidium sativum L.	1059
Limnophila indica (L.) Druce.	1037
Lindernia crustacea F. Muell.	1036
Melilotus indica (L.) All.	1024
Melilotus indica (L.) All.	1060
Mitrogyna parviflora (Roxb.) Kunth.	1040
Nicotiana plumbaginifolia Viv.	1079
Nothosaerva brachiata Wt.	1043
Nymphoides cristatum (Roxb.) Kuntze.	1052
Oryza sativa Linn.	1019
Oryza sativa Linn.	1106
Panicum paludosum Roxb.	1083

Paspalidium flavidum (Retz.) A.	1062
Paspalum distichum Linn.	1080
Paspalum scrobiculatum L.	1012
Phyla nodiflora (L.) Greene.	1088
Pisum sativum	1067
Physalis minima L.	1039
Polygonum plebeium R. Br.	1026
Polypogon monspeliensis (L.) Desf.	1017
Polypogon monspeliensis (L.) Desf.	1058
Potamogeton nodosus Poir.	1071
Potamogeton pectinatus L.	1057
Potentilla supina L.	1084
Potentilla supina L.	1085
Rostellaria prostrata C.B. Clarke	1014
Ruellia tuberosa L.	1002
Rumex dentatus Linn.	1027
Rumex dentatus Linn.	1064
Salvadora persica Linn.	1025
Scirpus litoralis Schrad.	1075
Scirpus roylei (Nees.) Parker.	1023
Scirpus roylei (Nees.) Parker.	1072
Scirpus tuberosus Desf.	1074
Scirpus tuberosus Desf.	1081
Setaria verticillata (Linn.) Beauv.	1096
Sida cordifolia L.	1034